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Revision of the Recent *Bullata* Jousseaume, 1875 (Gastropoda: Marginellidae) with the description of two new species

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ABSTRACT

The genus *Bullata* Jousseaume, 1875 is revised based on conchological characters. All known living species are endemic to Brazil. Two new species are herein described, *B. guerrinii* and *B. analuciae*. *Bullata guerrinii* is most similar to *B. largillieri* (Kiener, 1841) as both have an enlarged second columellar plication which overrides and fuses with the first, but differs in having a darker coloration, wider aperture, and spire only slightly apparent. *Bullata analuciae* has similar color pattern to *B. largillieri*, but differs in having clearly separate first and second columellar plications, a generally larger, thinner shell, a broad aperture and non-denticulated lip. The other 4 known species are described and discussed and a key for identification is presented. A cladistic analysis of *Bullata* was made using 22 conchological characters (53 states). The single most parsimonious tree obtained (length 37, CI = 81, RI = 69) is as follows: (*B. bullata* (*B. analuciae* ((*B. largillieri*, *B. guerrinii*) (*B. lilacina*, *B. matthewsi*)))). The monophyly of the genus is supported by 8 synapomorphies.

Additional key words: Volutoidea, Neogastropoda, new species, Brazil, phylogeny.

INTRODUCTION

The genus *Bullata* Jousseaume, 1875 includes species that live in tropical waters from the intertidal down to 70 m. Recent species of the genus, as it is currently defined (Coovert and Coovert, 1995), are endemic to the continental shelf off Brazil. Yet, its fossil record can be traced to the Miocene of Trinidad (Maury, 1925) and the Mio–Pliocene of the southeastern United States (Redfield, 1870; Olsson, 1916).

As with most Marginellidae, throughout its taxonomic history, species of *Bullata* were earlier referred to the genus *Marginella* Lamarck, 1799. The genus was first differentiated as a group by Swainson (1833) who erected the genus *Volutella*, a name preoccupied, however, by *Volutella* Perry, 1810 (= *Vasum* Röding, 1798). This designation was, nonetheless, widely used. In 1875, Jousseaume established *Bullata* as a replacement name for *Volutella* but put too much emphasis on the involute spire as a diagnostic character for included species. Thus, in Jousseaume's monograph, the genus was used to encompass species that later were assigned to other genera and families, such as *Closia* Gray, 1857, *Prunum* Herrmannsen, 1851, *Cryptospira* Hinds, 1844, *Granulina* Jousseaume, 1888; *Gibberula* Swainson, 1840; *Persicula* Schumacher, 1817 (the last 3 genera belong in the Cystiscidae). Coovert and Coovert (1995), in their recent taxonomic revision of the Marginellidae and Cystiscidae, provided a more refined diagnosis of the genus.

Similarly to what probably occurs with other marginellids, the two new species described herein have eluded Brazilian malacologists for a long time due to their limited ranges and subtly different conchological characters. Both species could easily be mistaken for *Bullata largillieri* (Kiener, 1841) due to somewhat similar color patterns.

This work is part of an ongoing revision of the Brazilian Marginellidae by the senior author. Institutional abbreviations used are: ANSP: Academy of Natural Sciences of Philadelphia, Philadelphia; BM(NH): The Natural History, London; BMSM: The Bailey-Matthews Shell Museum, Sanibel, Florida; GAC: collection of Gary A. Coovert; IBUFRJ, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro; MNHN: Muséum National d'Histoire Naturelle, Paris; MNRJ: Museu Nacional/Universidade Federal do Rio de Janeiro; MORG: Museu Oceanográfico "Prof. Eliézer de Carvalho Rios", Rio Grande; MZUSP: Museu de Zoologia, Universidade de São Paulo, São Paulo; PMC: collection of Paulo Márcio S. Costa, Rio de Janeiro; USNM: National Museum of Natural History, Smithsonian Institution, Washington.

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SYSTEMATICS

Family Marginellidae Fleming, 1828
Subfamily Marginellinae Fleming, 1828
Tribe Prunini Coovert and Coovert, 1995
Genus *Bullata* Jousseaume, 1875

Bullata Jousseaume, 1875: 167, 250, *nomen novum* for *Volutella* Swainson, 1833 (*non Volutella* Perry, 1810)

Marginella (*Volutella*) Swainson, 1833: (2)1, *Marginella* pl. 1 [type species: *Marginella bullata* Lamarck, 1822 = *Voluta bullata* Born, 1778; original designation] (*non Volutella* Perry, 1810)

Gibberulina Monterosato, 1884:139 (see Coovert, 1987: 27, for further details).

Type species: *Voluta bullata* Born, 1778; by tautonomy.

Diagnosis: Shell moderately large to very large for family, colored with bands or other patterns, narrowly to broadly obovate; spire immersed or nearly so; lip thickened, denticulation usually present, absent in some; posterior end of lip arched above apex; external varix present; varix groove adjacent to body whorl, distinctly colored; siphonal notch absent; parietal callus present to nearly obsolete in type species; columella with 4 strong plications occupying less than half the aperture but not crowded in anterior direction.

Description: Shell 14–98 mm in length, narrowly to broadly obovate (length: width ratio 1.53–1.83); surface glossy, unsculptured, with 4–5 whorls. Color pattern composed of indistinct darker spiral bands, with or without rows of irregular white spots. Spire immersed to very low and apparent, often covered by callus. Protoconch apparent to completely concealed. Outer lip moderately to heavily thickened, internally denticulated or smooth, with a distinct, colored external varix, particularly strongly colored in varix groove adjacent to the body whorl. Lip with or without a distinct, flattened, beveled area in anterior direction. Aperture narrow to moderately broad, wider in anterior direction, some species with an obscure to distinct trough or siphonal "gutter" (best seen in apical view). Parietal callus nearly obsolete to strongly developed; posterior callus nearly obsolete to strongly developed; left antero-ventral callus extending from the anterior end of varix to level of third plication, often resembling a fasciole. Columella straight to concave, with 4 strong plications; plications subequal, or the first and/or second strongly developed, sometimes fused; third and fourth plications confined to aperture or slightly emerging, distal ends truncate or gradually diminishing. Space between plications increases in posterior direction, fourth plication often remote. Plication angle increasing in posterior direction relative to longitudinal axis.

Remarks: Several authors (see species synonymy lists, *q.v.*) have variously combined *Bullata* and *Closia* Gray, 1857, apparently based on the superficial resemblance of shell shape, especially that of *B. lilacina* (Sowerby, 1846). *Closia* differs in a number of conchological characters, chiefly the very thin, very sharply formed plications that are strongly crowded in anterior direction. *Bullata*, on the other hand, has much thicker, rounded plications that are not nearly as crowded in anterior direction. The labial denticulation of *Closia* is sharply, regularly formed and widely spaced (i.e., separated by a distance greater than the thickness of a denticle). The labial denticulation in *Bullata* is irregularly formed and crowded or nearly absent. The columella in *Closia* is concave, resulting in a sinuous outline, while in *Bullata* the columella is more straight. *Closia* has a much more completely immersed spire and a tendency toward a much lighter shell. *Closia* is probably closely allied to *Ovaginella* (Coovert and Coovert, 1995: 87) and thus in the Austroginellini. *Bullata* has an oesophageal caecum just posterior to the nerve ring, type 6 radula (Coovert and Coovert, 1995: 56–57), and lacks the Valve of Leiblen, character states that allocate the genus placing it in the tribe Prunini. Also, these genera are restricted in their biogeography to specific oceanographic basins: *Bullata* to Southern West Atlantic and *Closia* to the Indian Ocean (Coovert and Coovert, 1995: 87). Thus, we consider *Closia* to be a separate and unrelated genus, which includes *C. sarda* (Kiener, 1834) as the type species, as well as *C. majuscula* (Martens, 1880) and *C. princeps* (Sowerby, 1901).

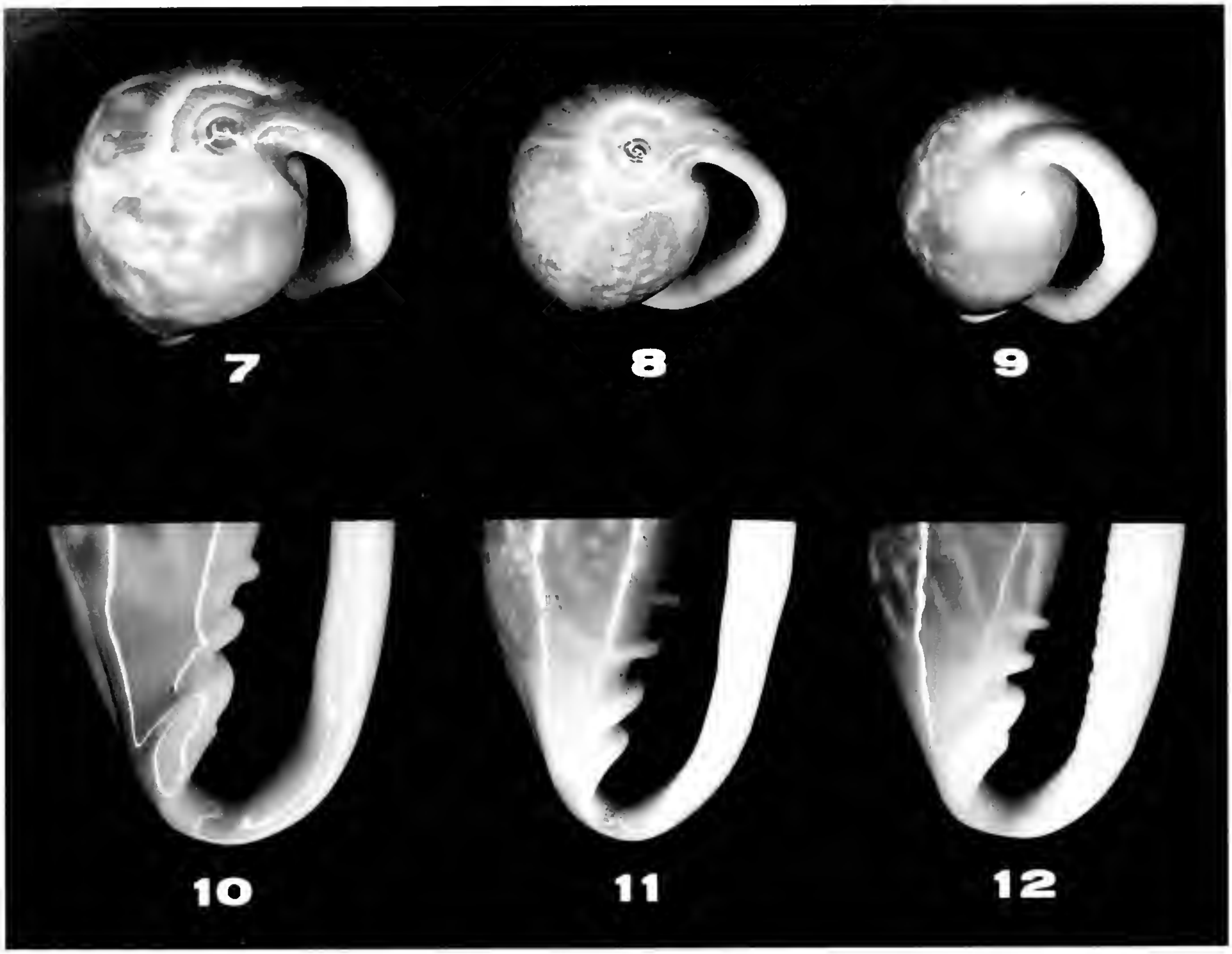
Cryptospira angustata (Sowerby, 1846) was included in *Bullata* by Jousseaume (1875: 251), due to the immersed spire. But most species of *Cryptospira* can be differentiated by their much stronger fasciole-like callus, much stronger and more numerous columellar plications that occupy more than half the aperture, and extensive callusing posterior to varix. Thus we consider *Cryptospira* to be a separate genus with a separate origin but within the Prunini, with distribution restricted to the Indo-Pacific Region (Coovert and Coovert, 1995: 93).

Although described as *Bullata lipei* Clover, 1990, we agree with Lipe and Sunderland (1991:15), and consider this a species of *Prunum*, probably a close relative of *Prunum rostratum* (Redfield, 1870). The narrow shape of the shells, the ventral area of the body whorl just posterior to the plications, which is built up by callus and forms a groove just posterior to the first plication, and the very reduced, remote fourth plication, are very similar in these two species. Also both species are from the Yucatan region of Mexico. The involute shell of *Prunum lipei* (Clover, 1990) with the posterior end of the lip arching above the spire, represents a combination of shell traits that appears in other marginellid genera and, although present in *Bullata*, is not a diagnostic character this genus.

Bullata guerrinii new species
(Figures 1, 7, 10)

Diagnosis: Color pattern of irregular, squarish cream spots; spire slightly but distinctly apparent, extremely

Figures 1–6. *Bullata* species in ventral and dorsal views. **1.** Holotype of *Bullata guerrini* new species. MNRJ 7818, length 27.0 mm, width 16.5 mm. **2.** Holotype of *Bullata analuciae* new species. MNRJ 7186, length 27.0 mm, width 18.4 mm. **3.** *Bullata bullata* (Born, 1778), IBUFRJ 8471, length 82.1 mm, width 45.2 mm. **4.** *Bullata largillieri* (Kiener, 1841), PMC 939, length 2[illegible] mm, width 13.4 mm. **5.** *Bullata lilacina* (Sowerby, 1846), PMC 476, length 24.5 mm, width 14.9 mm. **6.** *Bullata matthewsi* (Van Mol and Tursch, 1967), PMC 937, length 39.0 mm, width 22.9 mm.



Figures 7–12. *Bullata* species: spire, posterior labial insertion, and columellar structures. **7, 10.** Holotype of *Bullata guerrinii* new species. **8, 11.** Holotype of *B. analuciae* new species. **9, 12.** *B. largillieri* (Kiener, 1841), PMC 939.

low, dome-like, partially covered by posterior labial insertion and posterior parietal callus; aperture brown internally, becoming paler toward the lip; first and second plications distally fused, forming 1 strong plication ridge.

Description: Shell of medium size (25–29 mm in length), moderately heavy, obovate (length: width ratio 1.61–1.67, $\bar{x}$ = 1.639, s = 0.0199, n = 6), with approximately 4.5 whorls. Color pattern of irregular squarish cream spots, arranged in irregular axial rows, on purplish-brown background, crossed by 4 indistinct darker spiral bands (1 near suture, 2 narrower ones at midsection of body whorl, 1 near anterior end). Spire extremely low, dome-like, slightly but distinctly apparent, partially covered by posterior labial insertion and posterior parietal callus. Protoconch visible or partially so, dark-brown. Outer lip thickened internally, with distinct, heavy external varix, thinning abruptly in posterior direction, with indistinct, flattened, beveled area thinning evenly in anterior direction, labial denticulation very fine, obsolete to indistinct, varix groove excavated. Outer lip brownish-white, darkening toward varix groove. Aperture narrow, slightly wider than lip thickness when measured ventrally, wider in anterior direction and somewhat angled at posterior end. Aperture brown internally, becoming paler toward lip. Parietal wall convex with continuous ventral callus, thickening toward aperture, thinning abruptly along collabral line just outside aperture. Ventral callus extending in anterior direction, thinning but smoothly joining left antero-ventral callus. Posterior callus forming rounded mound separated from posterior lip insertion by notch. Left antero-ventral callus extending from anterior end of varix to level of fourth plication, with distinct furrow between second and third plications, and continuing as sharp, distinct, straight continuation of varix. Ventral callus whitish brown. Columella slightly concave, plications somewhat strong. First plication much weaker than second, both distally fused, forming 1 very strong plication ridge, separated from the parietal callus by distinct groove. Third plication stronger than fourth, weaker than plication ridge, extending

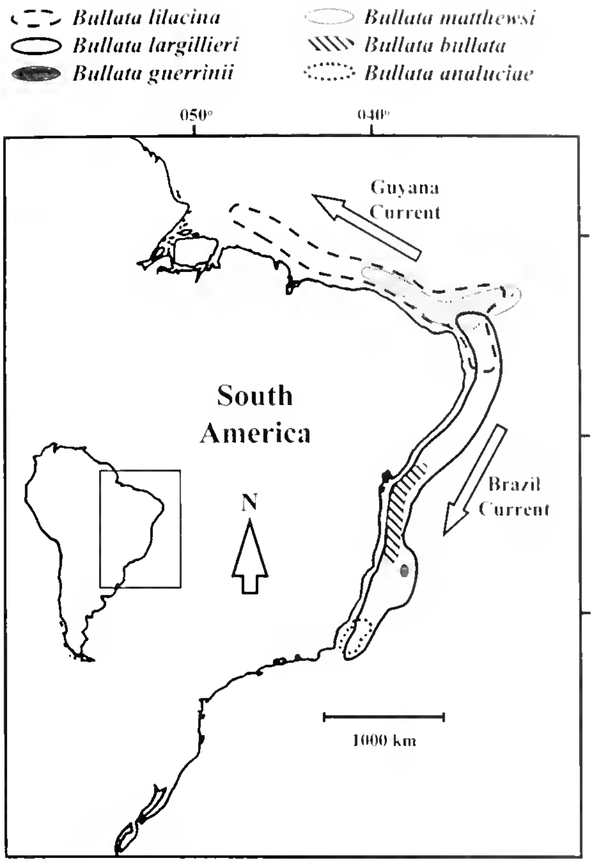


Figure 13. Geographic ranges of the living species of *Bullata*

slightly outside aperture; fourth plication confined to aperture. Space between plications increasing in posterior direction, with fourth plication somewhat remote (i.e., distance between third and fourth plications distinctly greater than distance between second and third). Third and fourth plications gradually narrowing distally.

Type material: Holotype, MNRJ 7818 (length 27.0 mm, width 16.5 mm); Paratypes: BM(NH) 1996417 (length 23.3 mm, width 14.2 mm); IBUFRJ 10000 (length 25.7 mm, width 15.4 mm); MNHN (length 29.8 mm, width 18.3 mm); MZUSP 28849 (length 26.1 mm, width 15.7 mm); USNM 890896 (length 24.4 mm, width 15.1 mm), all from 40 km NE off Alcobaça, Bahia State, Brazil, 10–35 m.

Type locality: Pedra da Lixa (17°41.5' S, 038°59' W), Parcel das Paredes, 27 km E off Caravelas, Bahia State, Brazil, 5–15 m.

Geographic range: Known from type locality, and, according to local fishermen, from reefs around Abrolhos Archipelago (figure 13).

Remarks: *Bullata guerrinii* is most similar to *Bullata largillieri* (Kiener, 1841) in their color patterns and fused first and second plications (figures 10, 12). But these species differ in their shell shape, general color, spire (figures 7, 9), ventral callusing, aperture width, shape of external lip, and shape of the third and fourth plications (figures 10, 12).

Bullata guerrinii is easily distinguishable from *B. bullata*, *B. lilacina* (Sowerby, 1846) and *B. matthewsi* (van Mol and Tursch, 1967), by its spotted color pattern, while the others have banded color patterns (figures 1–6).

For a summary of these differences, refer to dichotomous key included later in this paper.

Etymology: *guerrinii*: species dedicated to Mr. Ricardo Guerrini.

Bullata analuciae new species
(Figures 2, 8, 11)

Marginella (Closia) largillieri —Eisenberg, 1981: 126, fig. 8 (non Kiener, 1841).
Marginella largillieri —Abbott and Dance, 1986: 234, unnumbered fig. (non Kiener, 1841)
Bullata aff. *bullata* —Leal, 1990: 244
Bullata cf. *largillieri* —Lipe, 1991: 2–3, pl. 1, fig. 2.
Bullata sp.1 —Leal and Bouchet, 1991: 23.
Closia cf. *largillieri* —Bozzetti, 1996: 54, unnumbered fig.

Diagnosis: Color pattern of small irregular cream spots arranged in axial rows, evenly superimposed on caramel-brown background, crossed by 4 indistinct darker spiral bands; labial denticulation absent or reduced to very obscure undulations; aperture wide, broader than lip thickness when measured ventrally; first and second columellar plications completely separate, subequal in size. Third plication is subequal in size to first 2, fourth plication weaker and confined to aperture.

Description: Shell small to medium (15–38 mm in length), obovate (length:width ratio 1.49–1.70, $\bar{x}$ = 1.618, s = 0.0669, n = 18), with approximately 4 whorls. Surface glossy, without sculpture; color pattern of small, irregular cream spots arranged in axial rows, evenly superimposed on caramel brown background, crossed by 4 indistinct darker spiral bands (1 near suture, 2 narrower ones at mid-section of body whorl and 1 near anterior end). Spire almost completely immersed, flattened to slightly depressed, exposed but covered by glassy transparent callus, partially covered by posterior lip insertion and posterior parietal callus. Protoconch partially visible, large, dark-brown. Outer lip thickened internally, with distinct external varix, thicker medially and thinner toward extremities, lacking distinct, flattened, beveled area in anterior direction; labial denticulation absent or reduced to very obscure undulations; varix groove distinctly excavated. Outer lip white, externally darkening to bright brownish-orange in varix groove adjacent to body whorl. Aperture wide, broader than lip thickness when measured ventrally, curving in posterior direction, broadest in anterior direction. Aperture internally medium-brown with lilac stain at anterior end. Parietal wall convex with thin ventral callus wash that is thicker at anterior and posterior ends. Posterior callus in fully adult

shells forms peaked mound separated from posterior lip insertion by distinct gap. Left antero-ventral callus extends from anterior end of varix to level of third plication, producing sharp, distinct, and straight continuation of varix. Columella slightly concave, plications slender. First and second columellar plications completely separate, subequal in size. Third plication is subequal in size to first and second, fourth plication weaker and confined to aperture. Space between the plications increases in posterior direction, with fourth plication remote (i.e. distance between third and fourth plication distinctly greater than distance between second and third). Third and fourth plications gradually narrowing distally, ending in sharp points.

Type material: Holotype, MNRJ 7186 (length 34.7 mm, width 20.4 mm); Paratypes: ANSP 390361 (length 32.8 mm, width 19.3 mm); ANSP 399366 (length 27.7 mm, width 18.0 mm); ANSP 399995 (length 34.5 mm, width 20.4 mm); BM(NH) 1996071 (length 34.2 mm, width 20.9 mm); BMSM, 1006 (length 31.2 mm, width 19.8 mm); IBUFRJ 8463Paratype 3 (length 37.2 mm, width 23.3 mm); IBUFRJ 8464 (length 32.0 mm, width 20.1 mm); MNHN. (length 30.7 mm, width 19.0 mm); MNRJ 7187 (length 28.1 mm, width 16.8 mm); MORG 33311 (length 33.4 mm, width 21.0 mm); MORG 33312 (length 27.0 mm, width 18.1 mm); MZUSP 28243 (length 31.6 mm, width 20.0 mm); USNM 880120 (length 25.2 mm, width 16.9 mm), all from off Vitória (20°20' S, 040°00' W), Espírito Santo State, Brazil, 60–70 m, trawled by shrimp fishing boats on muddy sand bottom; GAC M2861 (length 33.6 mm, width 19.9 mm), off Vitória, Espírito Santo State, Brazil, 50–70 m, trawled by shrimp fishing boats on silty sand; AMNH 213931 (length 29.9 mm, width 18.0 mm), off Espírito Santo State, Brazil, 50 m; AMNH 213930 (length 30.5 mm, width 18.2 mm); GAC M1426 (length 30.3 mm, width 18.7 mm), both from off northern coast of Rio de Janeiro State, Brazil, 50 m, muddy bottom.

Type locality: Off Vitória (20°20' S, 040°00' W), Espírito Santo State, Brazil, 60–70 m, trawled by shrimp fishing boats on muddy sand bottom.

Geographic range: From the northern coast of Rio de Janeiro State to the central coast of Espírito Santo State, Brazil (figure 13).

Remarks: In color pattern *B. analuciae* is most similar to *B. largillieri* and *B. guerrinii*, but they differ in shell shape, spire form (figures 6, 7, 8), ventral callusing, aperture width, shape and thickness of external lip, and columellar structure (figures 10, 11, 12).

Bullata analuciae is most similar, in shell shape and columellar structure, to *B. bullata*, but they differ in the color pattern, spire form, ventral callusing, and aperture shape and width.

Bullata lilacina and *B. matthewsi* differ in color pattern and geographical range.

Etymology: This species is dedicated to Ana Lucia Rodrigues Peixoto who first collected most specimens aboard shrimp fishing boats.

Bullata bullata (Born, 1778)
(Figure 3)

Voluta bullata Born, 1778: 205–206. Type information could not be directly obtained, holotype formerly in the Musei Caesarei Vindobonensis, Vienna, but declared missing (Tomlin, 1917: 225); type locality: Indian Ocean [in error, endemic to Bahia State, Brazil]; Born, 1780: 218; Tomlin, 1917: 255.
Marginella bullata.—d'Orbigny, 1841: 415; Sowerby, 1846: 401, pl. lxxvii, figs. 158, 159; Petit, 1851: 55; Reeve, 1860: 52; Reeve, 1864, pl. 1; Redfield, 1870: 225; Weinkauff, 1879: 24, pl. 4, figs. 3, 4; Paetel, 1888: 191; Smith, 1945: 71, fig. 950; Rogers, 1951: 89, pl. 24, fig. 5; Dance, 1976: 193, unnumbered figure.
Voluta ovum Gmelin, 1791: 3448.
Marginella magna Swainson, 1822: appendix: 12.
Marginella (*Volutella*) *bullata*.—Swainson, 1833; Adams and Adams, 1853: 192; Tryon, 1882: 35, pl. 10, figs. 3, 4; Fischer, 1883: 602; Tryon, 1883: 173, pl. 55, fig. 61.
Marginella bellangeri Kiener, 1834: 27–28, pl. 9, fig. 43; Catlow and Reeve, 1845: 291; Reeve, 1860: 52.
Marginella cuvieri Deshayes, 1853: 75 (*Explication des Planches*); 1857–58: pl. 123, fig. 8; Redfield, 1870: 262.
Bullata bullata —Jousseaume, 1875: 250; Tomlin, 1817: 244; Coan, 1965: 189; Rios, 1970: 113, pl. 40; Oliveira *et al.*, 1972: 14; Rios, 1975: 117, pl. 35, fig. 506; Wagner and Abbott, 1978: 22003; Rios, 1985:121, pl. 42, fig. 537; Coovert, 1986a: 2; Coovert, 1986b: 3; Coovert and Lee, 1989: 4; Coovert and Coovert, 1990: 2, fig. 1; Rios, 1990: 8, fig.; Lipe, 1991: 2, pl. 1 fig. 10; Rios, 1994: 147, pl. 48, fig. 638; Bozzetti, 1994 p. 54; Coovert and Coovert, 1995: 92, fig. 66; Rosenberg, 1996, [gopher://erato.acnatsci.org:70/0R1815753-1816546-/.wasp/.text/waspgoph.cvt].
Bullata cuvieri (Deshayes, 1853). —Jousseaume, 1875: 251.
Marginella (*Volutella*) *bellangeri*.—Kobelt, 1878. 72, pl. 27, fig. 2.
Marginella (*Bullata*) *bullata*.—Thiele, 1929: 355, fig. 429; Eisenberg, 1981: 129, fig. 14.
Closia (*Bullata*) *bullata* —Wenz, 1943: 1376, fig. 3892.
Marginella (*Closia*) *bullata* —Morretes, 1949. 104
Marginella bullata —Santos, 1955: 113, unnumbered figure.

Diagnosis: Shell large (34–101 mm), slender; color pattern of numerous thin to very thin darker spiral bands crossed by thin axial lines on rosy-gray background; obsolete crenulation on outer lip; aperture wide, broader than lip thickness when measured ventrally; ventral callus reduced to obsolete wash.

Description: Shell large (34–101 mm), smooth, elongated, narrowly obovate (length:width ratio 1.51–1.96, $\bar{x} = 1.83$, $s = 0.0946$, $n = 25$), with about 5 whorls. Color pattern composed of numerous thin to very thin darker spiral bands crossed by thin, mostly pale or occasionally darker axial lines on rosy gray background (usually fading into pinkish-tan with time, in museum specimens). Axial lines are apparently associated with incremental growth lines. Spire immersed and covered by a vitreous callus, sometimes visible, rarely partly covered by lip insertion.

which imparts flattened to depressed shape to posterior end of shell. Protoconch darker than early teleoconch whorls, usually completely covered by vitreous callus. Outer lip thickened internally, with distinct external varix, thinner toward extremities, with an obscure, flattened, beveled area in anterior direction, and often abruptly thinned in anterior direction, labial denticulation usually reduced to obscure undulations, at most present as obsolete denticles. Varix groove generally filled forming wide, rounded, or flattened shelf. Outer lip white, externally darkening to orangish-brown, especially on varix groove adjacent to body whorl. Aperture wide, broader than lip thickness measured ventrally, curving in posterior direction, broadest in anterior direction. Aperture internally brown, becoming white toward lip. Parietal wall convex with thin ventral callus wash. Posterior callus nearly obsolete. Left antero-ventral callus extends from anterior end of varix to level of third plication in gradual curve toward columella, resembling a fasciole. Columella slightly concave, plications slender to somewhat heavy. First and second columellar plications separate to fused distally, subequal in size. Third plication is subequal in size to first and second plications, with fourth plication subequal to slightly weaker and confined to aperture. Space between plications increases in posterior direction, with fourth plication remote (i.e., distance between third and fourth plication distinctly greater than distance between second and third). Third and fourth plications gradually narrowing distally.

Material examined: Types of *Marginella cuvieri* Deshayes, 1853, MNHN unumbered, Bahia, Brazil; IBUFRJ 1540, off Salvador, Bahia State, Brazil, 5–10 m, B. Linhares col.; IBUFRJ 8471, off Salvador, Bahia State, Brazil, 5–10 m, B. Linhares col.; MZUSP 547, off Salvador, Bahia; MZUSP 15686, Mar Grande, Itaparica, Bahia State, Brazil, G. May, col.; MZUSP 27267, off Salvador, Bahia State, Brazil.

Geographic range: Endemic to Bahia State, Brazil (figure 13).

Remarks: *Bullata bullata* is most similar, in size and color pattern, to *B. matthewsi*, but they differ in background color, spire form, callus structure, aperture width, and labial denticulation. In addition, their geographical ranges are widely disjunct (figure 13).

See remarks under *B. guerrinii* and *B. analuciae*, and key for comparison with *B. bullata*.

Bullata bullata differs from *B. largillieri* and *B. lilacina* in size, shell shape, color pattern, structure of ventral callus, aperture width, and columellar structure.

Apparent spire, yellowish coloration and smaller size in original illustration of *Marginella cuvieri* Deshayes, 1853 seemed to indicate that this species was a senior synonym of *B. matthewsi*. But in examining types, it became clear that they were smaller discolored *B. bullata*, two of them with atypically apparent spires (but covered with callus). The broad medial white band shown in the original illustration was due to shell deterioration. This "variety" was later discussed by Sowerby (1846: 401, sp. 104; pl. 77, figure 159) who did not mention Deshayes's work.

Bullata largillieri (Kiener, 1841)
(Figures 4, 9, 12)

Marginella largillieri Kiener, 1841: 43–44, pl. 11, fig. 3 [Holotype not found, types were formerly deposited in Rouen Museum, but are now missing (P. Bouchet, personal communication, 1998). Type locality: Bahia, Brazil ["baie de Bahia" Kiener, 1841: 43, most probably Todos os Santos Bay)]; Catlow and Reeve, 1845: 292; Reeve, 1860: 52; Reeve, 1864, pl. VI, fig. 22 a, b; Redfield, 1870: 240; Tomlin, 1917: 275, Dance, 1976: 195 unnumbered figure.
Marginella l'argillieri.—Sowerby, 1846: 402, pl. lxxviii, figs. 178, 179, 180; Paetel, 1883: 31
Marginella largillierti.—Petit, 1851: 52; Weinkauff, 1879: 44, pl. 8, figs. 2, 3; Rios and Oleiro, 1968: 17, Oliveira *et al.*, 1981: 271.
Marginella (Volutella) largillieri.—Adams and Adams, 1853: 192; Kobelt, 1878: 72, pl. 27, fig. 9.
Marginella ovum Reeve, 1864: sp. 89, pl. XVIII, fig. 89a, b; Redfield, 1870: 247; Weinkauff, 1879: 65, pl. 12, figs. 6, 7; Paetel, 1888: 195
Marginella l'angillierti.—Paetel, 1869: 38
Closia largilleri.—Jousseaume, 1875: 255
Closia paros Jousseaume, 1875: 255 (*nomen novum* for *Marginella ovum* Reeve, 1865); Tomlin, 1917: 287.
Marginella (Closia) largillierti.—Tryon, 1882: 47, pl. 12, figs. 77, 78.
Marginella l'argillierti.—Paetel, 1888: 194
Marginella (Closia) largillieri.—Morretes, 1949: 104
Closia largillieri.—Rios, 1970: 114, pl. 40; Rios, 1975: 117, pl. 35, fig. 508, Wagner and Abbott, 1978: 22008
Closia largillere.—Oliveira *et al.*, 1972: 14.
Persicula (Closia) largillieri.—Rios, 1985: 122, pl. 42, fig. 542.
Persicula largillieri.—Leal, 1990: 171, 399, 417.
Marginella sp. 65.—Lipe, 1991: 2, pl. 1, fig. 12.
Bullata largillieri.—Lipe, 1991: 2, pl. 1, fig. 3, Rosenberg, 1996 [gopher://erato.acnatsci.org 70/0R1816546-1816945-/.wasp/.text/waspgoph.cvt].
Closia largillierti.—Bozzetti, 1992: 10.
Bullata largillierti.—Rios, 1994: 147, pl. 48, fig. 639

Diagnosis: Shell heavy, obovate to broadly obovate; color pattern of small, irregular cream spots arranged in axial rows, superimposed on light chocolate-brown background; spire completely immersed, covered by posterior labial insertion and posterior parietal callus; labial denticulation sharp and distinct; ventral callus heavy, continuous; aperture narrow; first and second plication distally fused, forming very strong plication ridge.

Description: Shell of medium size (14–29 mm in length), heavy, obovate to broadly obovate (length:width ratio 1.39-1.67, $\bar{x}$ = 1.561, s = 0.0595, n = 25). Color pattern of small, irregular cream spots arranged in axial rows, on light chocolate-brown background, crossed by 1–3 indistinct darker spiral bands (1 near suture, 1 at mid-section of body whorl, and 1 near anterior end, this latter sometimes absent). Spotting somewhat to distinctly reduced on dark spiral bands. Spire completely im-

mersed, partially to completely covered by posterior labial insertion and posterior parietal callus. Protoconch not visible. Outer lip heavily thickened internally, with distinct, heavy external varix, thicker medially and thinner toward extremities, especially in posterior direction, with indistinct, flattened, beveled area in anterior direction, labial denticulation sharp and distinct, composed of approximately 24–36 denticles, varix groove excavated. Outer lip white, externally evenly colored a creamy brownish-orange, only very slightly darker in varix groove adjacent to body whorl. Aperture narrow, narrower than lip thickness measured ventrally. Aperture internally pale-brown. Parietal wall convex with continuous heavy ventral callus, thickening toward aperture, abruptly diminishing along collabral line just outside aperture, forming almost planar surface tangential to whorl. Callus extending to columella, next to distal ends of third and fourth plications. Posterior callus in fully adult shells forming rounded mound separated from posterior lip insertion by distinct gap. Left antero-ventral callus extending from anterior end of varix to level of fourth plication, with distinct furrow between second and third plications and producing a somewhat rounded continuation of varix. Columella concave, plications heavy. First plication much weaker than second, distally fused, effectively forming 1 very strong plication ridge, separated from parietal callus by distinct groove. Third plication is slightly stronger than fourth, both slightly emerging from aperture. Space between plications increases in posterior direction, fourth plication not remote. Third and fourth plications abruptly truncated and expanded distally, where they meet parietal callus.

Material examined: IBUFRJ 8909, Rio do Fogo Beach, Rio Grande do Norte State, Brazil, L. Couto col.; MNRJ 5440, off Boipeba, Bahia State, Brazil; MNRJ HSL 4180, Barra Beach, Salvador, Bahia State, Brazil; PMC 939, off Salvador, Bahia State, Brazil, B. Linhares col.; GAC M2215, IBUFRJ 1469, off Itabapoana, Espírito Santo State, Brazil.

Geographic range: Rio Grande do Norte State to northern coast of Rio de Janeiro State, Brazil (figure 13).

Remarks: See remarks under *B. guerrinii*, *B. analuciae*, and *B. bullata*, and key for a comparison with *B. largillieri*.

Bullata largillieri is readily distinguished from *B. lilacina* and *B. matthewsi* by its distinctive color pattern, different columellar plications, and its more obovate shape.

A juvenile specimen examined (IBUFRJ 1469) shows second plication strongly angled toward and fused with the first, but plications are comparatively thin and sharp, and not yet heavily thickened. This juvenile shell has no external varix but it appears that it was just beginning to thicken the lip inside the aperture. Lip is thin, gradually beveled, and with a sharp edge, which is very narrowly opaque white externally. There is no trace of parietal callus.

Marginella ovum Reeve, 1865, renamed *Closia paros* Jousseaume, 1875, seems to represent *B. largillieri*, given mentions in the original description of its "curiously swollen" second columellar plication, immersed spire, narrow aperture, and denticulated lip.

Bullata lilacina (Sowerby, 1846)
(Figure 5)

Marginella lilacina Sowerby, 1846: 402, pl. lxxviii, figs. 176–177. Holotype, BM(NH) 1880.9.18.2, type locality unknown; Petit, 1851: 55; Reeve, 1865, pl. xiv; Redfield, 1870: 240; Weinkauff, 1879: 46, pl. 4, figs. 3, 4; Paetel, 1888: 194: Matthews and Rios, 1967: 72; Kempf and Matthews, 1968: 93; Matthews and Kempf, 1970: 5, Matthews and Matthews, 1979: 71; Abbott and Dance, 1986: 234, unnumbered figure.
Marginella (Volutella) lilacina.—Adams and Adams, 1853: 192.
Marginella (Closia) lilacina.—Tryon, 1882: 47, pl. 12, fig. 80.
Marginella (Volvarina) lilacina.—Morretes, 1949: 105.
Closia lilacina.—Jousseaume, 1875: 255; Rios, 1970: 114, pl. 40; Rios, 1975: 118, pl. 35, fig. 509; Wagner and Abbott, 1978: 22008; Bozzetti, 1992: 10.
Persicula lilacina.—Oliveira *et al.*, 1981: 270.
Persicula (Closia) lilacina.—Rios, 1985: 121, pl. 42, fig. 538; Mello and Perrier, 1986: 133.
Bullata lilacina.—Lipe, 1991: 2, pl. 1, fig. 1; Rios, 1994: 147, pl. 48, fig. 640; Rosenberg, 1996, [gopher://erato.acnatsci.org:70/0R1816945–1817292-/.wasp/.text/waspgoph.cvt].

Diagnosis: Shell broadly obovate; color pattern of 2 pale-rose bands on rosy-brown background, outer lip white, externally pale- to dark-lilac; outer lip with distinct, flattened, beveled area in anterior direction, abruptly thinning in anterior direction forming siphonal "gutter"; first plication somewhat higher in ventral profile.

Description: Shell of medium size (19–33 mm in length), broadly obovate (length:width ratio 1.39–1.59, $\bar{x}$ = 1.533, s = 0.0573, n = 25). Color pattern of 2 pale-rose medial spiral bands, and numerous, thin darker indistinct spiral lines, crossed by thin, mostly pale or occasionally darker axial lines on rosy-brown background. Spiral lines absent on medial spiral bands, usually fading in collection specimens. Axial lines apparently associated with incremental growth lines. Spire immersed, mostly covered by callus, partially covered by posterior lip insertion and posterior parietal callus. Protoconch completely covered to barely visible, dark. Outer lip heavily thickened internally, narrowing rather abruptly in anterior direction and in posterior direction, with distinct, flattened, beveled area in anterior direction; abrupt anterior thinning of lip effectively forming siphonal "gutter" (best seen in apical view). Labial denticulation distinct, fine to coarse, composed of approximately 20 denticles. Varix distinct, heavy, varix groove deeply excavated. Outer lip white, externally pale- to dark-lilac, orangish-brown in varix groove adjacent to body whorl. Aperture narrow to moderately narrow, narrower than lip thickness when measured ventrally, broadest at level of plications, narrowing in anterior direction. Aperture

internally lilac with lilac stain at anterior end. Parietal wall convex with continuous, moderately heavy ventral callus, thickening toward aperture, thinning along indistinct collabral line just outside aperture, reaching fourth plication, usually indistinctly transversely undulated, extending to columella as a wash. Posterior callus in fully adult shells forming very low, rounded mound barely separated from posterior lip insertion by indistinct gap. Left antero-ventral callus extending from anterior end of varix to level of third plication as heavy wash, somewhat resembling indistinct fasciole, with lilac coloration, and slight furrow between second and third plications. Columella slightly concave, plications heavy. First and second columellar plications completely separate, subequal in size, and slightly stronger than third and fourth, first somewhat higher in ventral profile (best seen in lateral view). Third plication is subequal in size to fourth, both slightly emerging from aperture. Space between plications increasing in posterior direction, with fourth plication not remote. Third and fourth plications truncated and slightly expanded distally.

Material examined: AMNH 194277, off Fortaleza, Ceará State, Brazil; MNRJ 4175, Poço Beach, Paraíba State, Brazil; MNRJ HSL 4176, Camocim, Ceará State, Brazil; PMC 476, off Fortaleza, Ceará State, Brazil; IBUFRJ 8924, off Rio do Fogo, Rio Grande do Norte State, Brazil, 5–6 m, 04/1997; MZUSP 16339, off Fortaleza, Ceará State, Brazil; MZUSP 29716, off Fortaleza, Ceará State, P. Montouchet col., *ex-pisce Amphichthys cryptocentrus* (Valenciennes, 1837).

Geographic range: Amapá State to Ceará State, Atol das Rocas, Brazil (figure 13).

Remarks: Although *B. lilacina* has been reported from coast of Bahia (Rios, 1994), all specimens collected in Bahia that we observed, were in fact bleached *B. largillieri*, a species easily recognizable by its columellar structure.

The color pattern of *B. lilacina* in most preserved shells seems to consist of only 2 wide whitish bands. The examination fresh-collected shells (IBUFRJ 8924) revealed thin and numerous spiral and axial lines, which apparently fade with passing of time.

Bullata lilacina differs from *B. matthewsi* in the spire form, and structure of parietal callus and columella. For comparison with other species, see previous remarks and key.

Bullata matthewsi (van Mol and Tursch, 1967)
(Figure 6)

Marginella (Prunum) matthewsi van Mol and Tursch, 1967: 196–197, fig. 1, holotype: Stanford University Paleo-Type Collection 9856, type locality: off Fortaleza, Ceará State, Brazil, 36 m, *ex-pisce Amphichtys cryptocentrus* (Valenciennes, 1837).

Marginella matthewsi —Matthews and Rios, 1967: 72; Kempf and Matthews, 1968: 93; Matthews, 1968: 248; Abbott and Dance, 1986: 235, unnumbered figure; Matthews and Matthews, 1979: 71.

Prunum matthewsi —Wagner and Abbott, 1978: 22009.

Bullata matthewsi —Rios, 1970: 113, pl. 40; Rios, 1975: 117, pl. 35, fig. 507; Rios, 1985: 121, pl. 42, fig. 538; Rios, 1990: 9, unnumbered figure; Lipe, 1991: 2, pl. 1 fig. 4; Bozzetti, 1994: 54, fig. 1; Rios, 1994: 147, pl. 48, fig. 638; Rosenberg, 1996, [gopher://erato.acnatsci.org:70/0R1817292-1817496-/wasp/text/waspgoph.ext].

Diagnosis: Shell moderately large; color pattern of numerous thin to very thin tawny- to brownish-orange spiral bands crossed by numerous axial lines on pale-orange background; spire slightly but distinctly apparent; outer lip in anterior direction with very distinct, flattened, broadened, beveled area and distinct anterior trough or siphonal "gutter"; parietal wall with continuous, thin but distinct, ventral callus; first columellar plication distinctly larger and thicker than other 3.

Description: Shell moderately large (39–53 mm in length), obovate (length:width ratio 1.65–1.71, $\bar{x}$ = 1.681, s = 0.0211, n = 7), with 4.5–5 whorls. Color pattern of numerous thin to very thin tawny- to brownish-orange spiral bands crossed by thin, mostly pale or occasionally darker axial lines on pale-orange background. Two medial spiral bands of less dense coloration present. Axial lines apparently associated with incremental growth lines. Spire distinctly apparent, extremely low, dome-like, partially covered by posterior lip insertion and to a limited extent by posterior parietal callus. Protoconch mamillated, completely visible. Outer lip thickened internally, with distinct external varix, rather abruptly narrowed in posterior direction, with very distinct, flattened, broadened, beveled area in anterior direction; abruptly thinning in anterior direction, effectively forming a distinct trough or siphonal "gutter" (best seen in apical view), labial denticulation indistinct to distinct, fine to coarse, composed of approximately 27–30 denticles; varix groove distinctly excavated. Outer lip white, externally pale orange-cream, darkening to a pale brownish-orange in varix groove adjacent to body whorl. Aperture wide, broader than lip thickness measured ventrally, curving in posterior direction, broadest in anterior direction. Aperture internally nearly white, darker banding showing through very faintly. Parietal wall convex, with thin, but distinct and continuous ventral callus, forming very indistinct collabral ridge just inside aperture, extending to columella as a wash. Second indistinct collabral callus ridge present further inside aperture and abruptly ending just posterior to fourth plication, leaving distinct gap between them. Profile of collabral ridge even with the tops of the plications. Posterior callus in fully adult shells forming indistinct, low, rounded mound barely separated from posterior lip insertion by indistinct gap, and continuing in short arc toward aperture. Left antero-ventral callus extending from anterior end of varix to level of third plication as heavy deposit somewhat resembling indistinct fasciole, with somewhat distinct furrow between second and third plications. Columella nearly straight, plications strong. First columellar plica-

tion distinctly larger and thicker than other three, distinctly raised in ventral profile (best seen in lateral view), broadened, flattened, and abruptly merging with anterior edge. First and second columellar plications completely separate. Posterior three plications subequal in size, all emerging from aperture to progressively greater extent in anterior direction. Space between plications subequal, with fourth plication not remote. Posterior three plications gradually narrowing distally.

Material examined: Paratype, AMNH 134492, off Mucuripe, Ceará State, Brazil; PMC 939, off Fortaleza, Ceará State, Brazil; IBUFRJ 8925, off Fortaleza, Ceará State, Brazil; GAC M1325, off Fortaleza, Ceará State, Brazil; GAC M2704, off Fortaleza, Ceará State, Brazil; MZUSP 27308, off Fortaleza, Ceará State.

Geographic range: Maranhão State to Rio Grande do Norte State, and Fernando de Noronha Island (figure 13).

Remarks: *Bullata matthewsi* has a distinctly apparent spire, similar to that of *B. guerrinii* but they differ in spire height, color pattern, color patter. For comparison with congeneric species see specific remarks above and dichotomic key.

PHYLOGENY AND BIOGEOGRAPHY

Preliminary results of a cladistic analysis of the genus *Bullata*, using conchological characters, are reported; further analysis using anatomical data is intended and will be published at the earliest opportunity.

In this analysis, 22 conchological characters with a total of 53 states were used (Appendix). Character polarization was done through outgroup comparison method (Maddison *et al.*, 1984). The type species of *Prunum* Herrmannsen, 1850 [*P. prunum* (Gmelin, 1791)] was selected since this genus was proposed as the sister group to *Bullata* by Coovert and Coovert (1995: 92). The cladogram was calculated using Tree Gardener 2.2 software (Ramos, 1998) which is basically a graphic interface for Hennig86 (Farris, 1988).

A single most parsimonious tree (figure 14) was obtained (length = 37, CI = 81, RI = 69). The monophyly of *Bullata* (node 1) is sustained by 7 synapomorphies. Node 2, containing all species *Bullata* except *B. bullata*, is sustained by 2 synapomorphies (presence of posterior callus mound, partially thickened ventral callus, spotted color pattern). Node 3 is sustained by 6 synapomorphies (very thick external lip, distinct labial denticulation, beveled area on external lip, narrow aperture, furrow on anterior callus, fourth plication not remote). Node 3 gives origin to 2 branches, one with *B. matthewsi* and *B. lilacina* as terminal species, the other with *B. largillieri* and *B. guerrinii*. Node 4 is defined by the presence of siphonal gutter, ventral callus completely thickened, larger first plication, and reversion of color pattern to white spots on a brown background. Node 5 is sustained by the labial coloration that extends beyond the varix

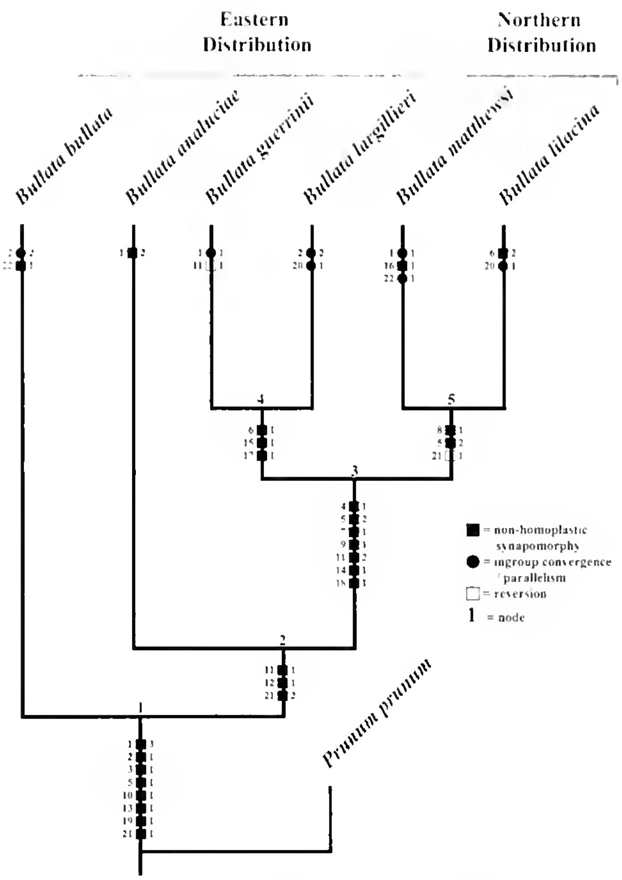


Figure 14. Single most parsimonious phylogenetic tree obtained from cladistic analysis of species of *Bullata* based on shell characters. *Prunum prunum* (Marginellidae) is the outgroup. See Appendix 1.

groove, small first plication and an enlarged second plication fused with first one.

Our feeling before the analyses was that *B. bullata* and *B. matthewsi* would group as sister taxa, due to similarities in size and color pattern. But the several sinapomorphies of nodes 2, 3, and 5, not shared by *B. bullata*, grouped *B. matthewsi* as sister species of *B. lilacina*.

The character optimization used in colour pattern (21) is only one of two equally parsimonious interpretations. Another possibility would be that the spotted pattern appeared as a parallelism between *B. analuciae* and node 4.

Coovert (1986c) proposed that the direct mode of development within a benthic egg capsule present in the Marginellidae would greatly reduce the dispersal abilities of its species, confining the distribution of species to a single zoogeographic province and many with even narrower distributions within these provinces. Scheltema (1989) found that there is significant relationship between the lack of planktonic larvae and distribution range. The distribution of the species of *Bullata* confirms these statements,with the very narrow distribution ranges of *B. bullata*, *B. analuciae*, and *B. guerrinii* and the relatively wider, but still confined to parts of the Brazilian coast, distributions of *B. largillieri*, *B. lilacina*, and

B. matthewsi. However, some capabilities for non-larval dispersal might be present, most probably by rafting of egg capsules and juveniles (Scheltema, 1989; Leal and Bouchet, 1991), since these three last species were able to colonize, respectively the Vitória Seamount (Leal, 1990), and Atol das Rocas and Fernando de Noronha Archipelago (Matthews and Kempf, 1970). All of these localities are separated from the continental shelf by depths greater than 2000 m, with Atol das Rocas and Fernando de Noronha, separated by distances greater than 300 km.

The geographic distribution of the genus along the Brazilian coast (figure 13) suggests two major patterns of distribution, with a slight overlap due to the extensive ranges of *B. largillieri* and *B. lilacina*: a northern species group, comprising *B. matthewsi* and *B. lilacina*; and a eastern species group, comprising *B. bullata*, *B. analuciae*, *B. largillieri* and *B. guerrinii*. The resulting cladogram is congruent, to a certain extent, with these geographic groups. The northern group corresponds to node 5. The eastern group is paraphyletic and consists of node 4 plus *B. analuciae* and *B. bullata*

These patterns appear to follow two major oceanographic current patterns present along the Brazilian coast: the northern group, associated with the Guyana current and the eastern group, associated with the Brazil current. It is possible that the divergent currents along with intracapsular mode of development may have contributed to isolate northern and eastern populations, facilitating speciation events.

Key to species of *Bullata*:

1a. Shell with distinct cream spots on caramel- or dark-brown background and with faint spiral banding 2

1b. Shell lacking cream spots, color pattern of few to many bands 4

2a. First and second columellar plications completely separate, subequal in size; parietal callus restricted to posterior end, not forming collabral ridge; aperture much broader than lip thickness; fourth plication remote (i.e. distance between third and fourth plication distinctly greater than distance between second and third); lip lacking denticulation, moderately thickened .... *Bullata analuciae* new species

2b. Second columellar plication greatly enlarged, fused with first; parietal callus moderate to heavy, forming weak to distinct collabral ridge; fourth plication not remote 3

3a. Spire completely immersed, usually covered by posterior labial insertion; aperture narrower than lip thickness, only slightly broader in anterior direction; parietal and other ventral callus white or nearly so; lip greatly thickened; third and fourth plications distinctly truncate and expanded at distal ends ..... *Bullata largillieri* (Kiener, 1841)

3b. Spire not immersed, slightly apparent, protoconch exposed; aperture as broad or broader than lip thickness medially, distinctively broader in anterior direction; parietal and other ventral callusing brown-tinged; lip moderately thickened; third and fourth plications gradually narrowing distally, ... *Bullata guerrinii* new species

4a. Shell smaller, 19–33 mm in length; color rosy-brown with 2 distinct light pink, broad bands; lip strongly denticulate; aperture narrower than lip thickness; third and fourth plications distinctly truncate at distal ends; lip strongly denticulate, greatly thickened; color pattern of 1 or 2 broad spiral color bands .... *Bullata lilacina* (Sowerby, 1846)

4b. Shell larger, 34–98 mm in length; color grayish-to orange-brown, without distinct broad spiral bands, with numerous distinct thin lines of varying thickness; lip at most weakly denticulate; aperture much broader than lip thickness; third and fourth plications gradually narrowing distally, ending in sharp points; color pattern of numerous, small spiral bands 5

5a. Lip weakly crenulated, with a flattened, broadened area in anterior direction, forming a weak siphonal "gutter"; spire slightly but distinctly apparent; first plication much stronger than other plications and distinctly higher in profile; fourth plication not remote, distance between third and fourth at most only slightly greater than distance between second and third .... *Bullata matthewsi* (van Mol and Tursch, 1967)

5b. Lip at most faintly crenulated, lacking flattened area in anterior direction; anterior 2 columellar plications subequal in size; spire immersed, apex flattened to depressed, usually covered; first plication as strong as or weaker than other plications, not higher in profile; fourth plication remote .... *Bullata bullata* (Born, 1778)

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Appendix 1. Character list and table.

Character 1. Spire shape, nonadditive, 4 steps, CI = 75, RI = 0
[0]—Apparent, conic, very low; [1]—Apparent dome-like; [2]—Involute flat; [3]—Involute, sunk.
Character 2: Posterior labial insertion, nonadditive, 3 steps, CI = 66, RI = 0
[0]—on body whorl; [1]—posterior to body whorl; [2]—covering apex.
Character 3: Varix, nonadditive, 1 step, CI = 100, RI = 100
[0]—narrow; [1]—wide.
Character 4. Lip thickness, 1 step, CI = 100, RI = 100
[0]—thick; [1]—very thick;
Character 5: Labial denticulation, nonadditive, 2 steps, CI = 100, RI = 100
[0]—absent; [1]—crenulated; [2]—distinct;
Character 6: Labial coloration, nonadditive, 2 steps, CI = 100, RI = 100
[0]—restrict to varix groove; [1]—extending ventrally; [2] − 3 colors;
Character 7: Anterior beveled area on external lip, 1 step, CI = 100, RI = 100
[0]—absent; [1]—present;
Character 8: Siphonal gutter, 1 step, CI = 100, RI 100
[0]—absent; [1]—present;
Character 9: Aperture width, 1 step, CI = 100, RI = 100
[0]—wide;[1]—narrow;
Character 10: Ventral callus, 1 step, CI = 100, RI = 100
[0]—absent; [1]—present very sinuous;
Character 11. Callus thickness, additive, 3 steps, CI = 66, RI = 0
[0]—thin; [1]—thick locally; [2]—thick all over;
Character 12. Posterior callus mound, 1 step, CI = 100, RI = 100
[0]—absent; [1]—present;
Character 13: Anterior callus, 1 step, CI = 100, RI = 100
[0]—simple; [1]—fasciole like;
Character 14: Furrow on anterior callus between second and third plications, 1 step, CI = 100, RI = 100
[0]—absent; [1]—present;
Character 15. first plication size, nonadditive, 2 steps, CI = 100, RI = 100
[0]—subequal; [1]—small; [2]—large;
Character 16: first plication in ventral profile, 1 step, CI = 100, RI = 100
[0]—normal; [1]—raised;
Character 17: second plication, 1 step, CI = 100, RI = 100
[0]—subequal; [1]—larger fused with first.
Character 18: fourth plication, 1 step, CI = 100, RI = 100
[0]—remote; [1]—not remote;
Character 19: False fifth plication, 1 step, CI = 100, RI = 100
[0]—present, [1]—absent;
Character 20: Shape of distal end of plications, 2 steps, CI = 50, RI = 0
[0]—thin evenly; [1]—truncate;
Character 21. Color pattern, nonadditive, 4 steps, CI = 50, RI = 0
[0]—few wide bands, [1]—many thin wide bands crossed by axial lines; [2]—spotted on wide bands;
Character 22: Size, 2 steps, CI = 50, RI = 100.
[0]—small to medium; [1]—large;

Reproduction and brooding of *Crepidula argentina*, Simone, Pastorino and Penchaszadeh, 2000 (Gastropoda: Calyptraeidae)

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ABSTRACT

Crepidula argentina is a protandric hermaphrodite that undergoes complete sex change. Males develop a mature gonad when the shell length is 4 mm. Sex change begins when shell length is around 8 mm and continues until 11 mm, when the first pre-vitellogenic oocytes are found. The minimum and maximum shell lengths for a brooding female are respectively 15 and 36 mm. There is a well-defined seasonal reproductive cycle; females brood between August and April. Females brood between 10 and 46 (mean 25) egg capsules per egg mass. The intracapsular fluid is translucent and viscous in recently laid capsules but becomes less dense closer to hatching. Neither nurse eggs nor cannibalism have been observed The mean number of eggs per mass was 5600 ± 3300. The egg capsules have a mean width of 2.1 mm (SD = 0.03 mm, N = 52), and a mean length of 2.4 mm (SD = 0.04 mm, N = 52). Each egg capsule contains about 320 embryos. The uncleaved egg diameter is about 170 μm. All eggs develop synchronously in the same brood The embryos hatch as planktotrophic veligers with a shell length of 190–230 μm and a bilobed velum about 160 μm in width. The mean size of the egg capsules, number of embryos per egg capsule, and number of embryos per brood are positively correlated with female shell length.

Additional key words: protandry, reproductive cycle, seasonality, encapsulation patterns, southwest Atlantic Ocean.

INTRODUCTION

Protandry is the most common kind of hermaphroditism among gastropods (Coe, 1938a). Protandry could be favored when female egg production increases with female size, while male reproductive success is independent of size (Collin, 1995). There is not an optimal size for sex change below which all the individuals are males and above which the individuals are females; instead, there is a range of sizes in which sexes overlap (Coe, 1938a; Heller 1993; Collin, 1995).

In general, calyptraeids have a protandric reproductive cycle with a similar sequence of sexual phases (Kükenthal, 1925). Youngest individuals are males and are usually not larger than few millimeters. The oldest individuals are larger than a centimeter. They become females after a transition period that depends on the species. Calyptraeids are characterized by the production of eggs that are brooded in bunches of stalked egg capsules attached either to the foot or to the substratum under the female. Each egg capsule has a thin membrane and a peduncle, which fixes it to the substratum. Hatching of planktonic veligers takes place in some species and of crawling juveniles in others (Hoagland, 1986).

Traditionally the taxonomy of species of the genus *Crepidula* was based exclusively on shell characters (i.e., Parodiz, 1939; Hoagland, 1977). The substratum has a great influence on the shell form of gastropods of sessile habits, making shell-based taxonomy difficult. Hence it becomes important to include other traits, such as anatomical and reproductive characters, in species characterizations.

The type of embryonic development is species-specific (Hoagland and Ponder, 1998). In some species few eggs develop and the rest of them remains uncleaved, becoming nurse eggs: this is the case of *C. dilatata* Lamarck, 1822 (Gallardo, 1979; Chaparro and Paschke, 1990) and *C. philippiana* Gallardo, 1977 (Gallardo, 1996), all from Chile. In the latter species, only one crawling juvenile hatches from each egg capsule. Egg capsules in other species contain only developing embryos immersed in a fluid (Hoagland, 1986).

Crepidula argentina Simone, Pastorino and Penchaszadeh, 2000, was described as a new species from material obtained for the present study. In it, we characterize the seasonality of reproduction, the relationship between sex change and size, minimum size at brooding, number of egg capsules per brood, the number of embryos per egg capsule, mean egg capsule size, uncleaved egg diameter, hatching stage, and the presence or absence of nurse eggs in *C. argentina*

MATERIAL AND METHODS

Characterization of sexual stages according to the size: Around 25 individuals per month were collected

These were found attached to shells of the mussel *Mytilus edulis platensis* d'Orbigny, 1846, from material landed by commercial fisheries at Mar del Plata harbor. The mussel banks are distributed in a patchy fashion on the continental shelf off the Province of Buenos Aires, from Querandí lighthouse to Necochea, between 35 and 50 m depth on mixed bottoms of sand and shell debris (Penchaszadeh, 1974).

The shell length of each individual was measured within 0.1 mm precision. The soft parts were preserved in Bouin's solution.

To study gonad development, 30 individuals were collected in January 1999 with size intervals of approximately 1 mm, and their gonads sectioned and stained with haematoxylin-eosin.

To confirm results from the macroscopic observation of gonads, the reproductive stage (as the proportion of sexual cells in different stages of development), or degree of gonad development, was examined through histological sections each month in ten females of more than 20 mm shell length.

Characterization of the reproductive season: The minimum shell length at which individuals brood was used as a minimum threshold for female reproductive capacity. A count of the number of broods per sample gave the monthly proportion of total brooding females. These data were contrasted with published bottom temperature data for the mussel beds area (40–50 m; 37°–38°30′ S, 56°–57°50′ W) (Ramirez *et al.*, 1973; Carreto *et al.*, 1998).

Characterization of broods and larvae: The egg capsules were fixed in 4% formalin in seawater and preserved in 70% alcohol. A total of 52 broods was studied. From each egg mass, 5 egg capsules were randomly selected for length and width measurements under a Zeiss stereoscopic microscope with a 0.1 mm precision ocular micrometer. The number of embryos was counted and the mean and standard deviation were calculated for each variable. A Kruskal-Wallis test was carried out between initial number of eggs per capsule and the number of pre-hatchlings per capsule in order to test the absence of nurse eggs or cannibalism.

We measured the diameter of 10 eggs per egg capsule, from 5 egg masses found with uncleaved eggs.

Simple linear regressions type 2 following natural logarithmic (ln) transformations were used to test the possible correlations between female shell length and the number of egg capsules per brood, the number of embryos per egg capsule, the mean egg capsule length and width

In addition to the preserved material we collected seven egg masses to describe the hatching stage. These were kept in a non-circulating aerated artificial marine water aquarium with 35‰ of salinity and temperature between 20 and 22°C. Hatchlings were measured with a digital video system attached to a Zeiss microscope.

The shell length at metamorphosis (protoconch) of young male individuals 4–6 mm length was measured using SEM.

RESULTS

Reproductive stages and shell length: Males are already functional when they attain approximately 4 mm in length. At this stage they have sexual cells at different degrees of development in the same spermatic follicle (figures 1–2).

Spermatogenesis diminishes when the individual reaches 8 mm in shell length and intrafollicular absorption begins at this stage (figure 3). The spermatozoids move to the seminal vesicle and the remaining spermatic cells suffer cytolysis and orange-yellow lipid vesicles appear.

The penis is located behind the right tentacle and is characterized by a filament on the distal tip; sperm groove was not observed (figure 4). Generally the penis gets reabsorbed simultaneously with the male gonadal structures. This process is usually completed when the size of the individual reaches 11 mm shell length. Nevertheless, we observed a case of an 11.8 mm length individual that retained a well-developed penis (figure 5) but in which histological sections revealed a female gonad with vitellogenic oocytes (figure 6).

The female genital papilla is generally visible in individuals of more than 10.3 mm in shell length.

Vitellogenesis begins at 11 mm shell length but females are not reproducing until they reach 14.5 mm. When they reach this size the animal holds a stock of mature oocytes and is able to brood. This was corroborated through histological sections of females collected monthly. Oocytes at different stages of maturation were found in all cases (figure 7).

After laying an egg mass, a stock of late vitellogenic oocytes is retained in the follicles, and re-absorption of oocytes was not detected.

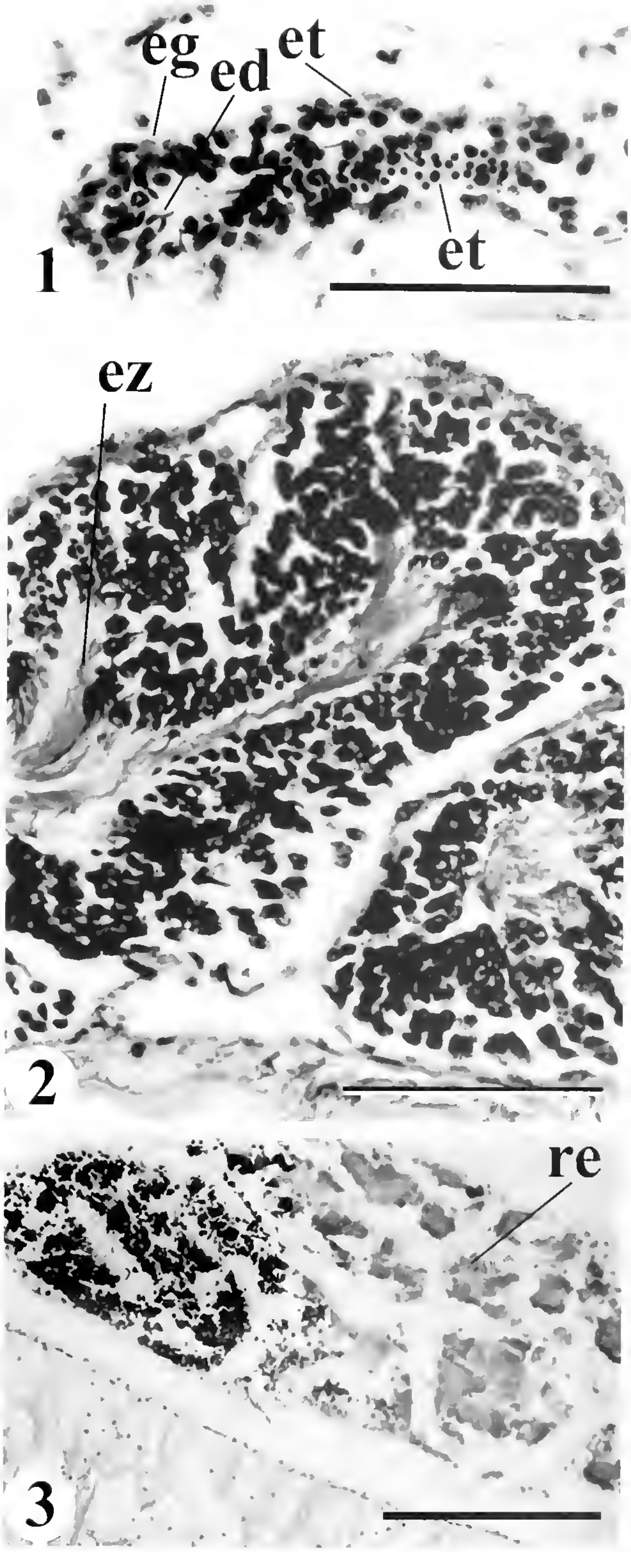
The largest brooding female was 36 mm shell length and the largest female 38.5 mm; both contained late vitellogenic oocytes.

Reproductive season, broods, larvae, and size at settlement: The study of 52 broods showed that each egg mass consists of 10–46 egg capsules (mean = 25, SD = 9, N = 52).

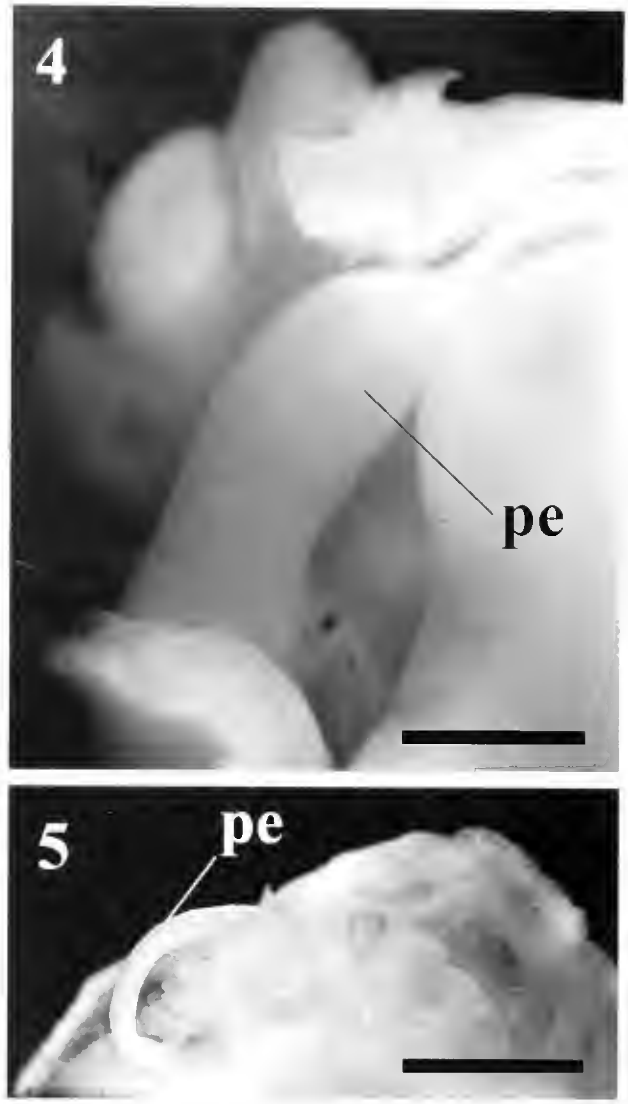
The reproductive season runs from August to April. Small females (14–20 mm) lay egg capsules only between September and February, while larger females reproduce during the entire reproductive season (figure 8).

The egg capsules are triangular with rounded edges, transparent, colorless, and bilaterally compressed (figure 9). In live egg capsules, the capsule walls are extremely delicate and often break when handled. The walls have a transparent double membrane and an attachment peduncle in their proximal extremity. The capsules measure 2.4 mm width (SD = 0.4 mm, N = 52) and 2.1 mm length (SD = 0.3 mm, N = 52), excluding the peduncle.

There is positive correlation between the ln-transformed egg capsule size (width and length) and the ln-



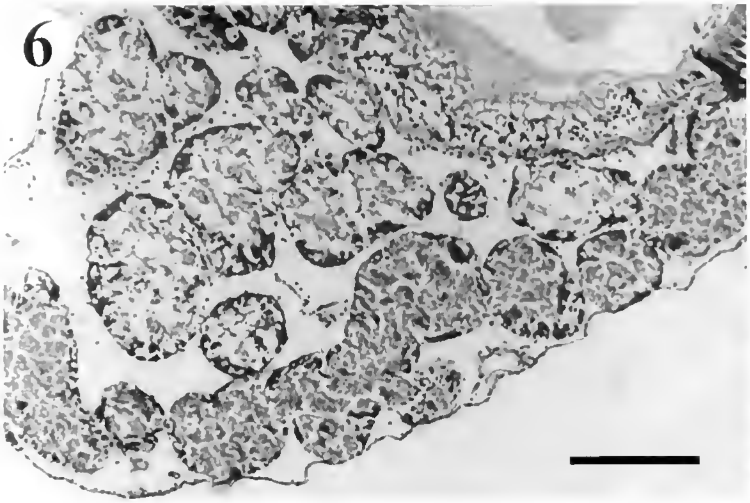
Figures 1–3. Light micrographs of *Crepidula argentina* testis. **1.** Spermatic follicle of a 4.7 mm male, containing cells in different degrees of development, eg: spermatogonial cell, et: spermatocites, ed: spermatide. Scale bar = 80 μm. **2.** View of a spermatic follicle of a 10.4 mm male containing a large proportion of spermatozoids (ez). Scale bar = 100 μm. **3.** View of a 7.7 mm male gonad in re-absorption phase (re) containing late spermatogenesis cells. Scale bar = 220 μm.

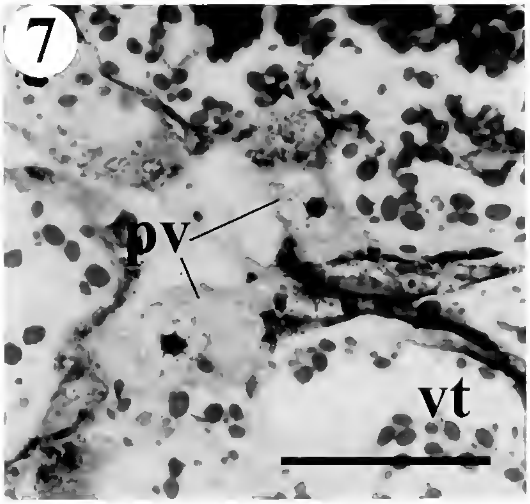


Figures 4–5. *Crepidula argentina.* **4.** Detail of the distal end of the penis (pe) of a 4.7 mm male. Scale bar = 0.5 mm. **5.** View of the penis (pe) of an individual of 11.8 mm whose gonad has developed oocytes. Scale bar = 2 mm.

transformed length of the female ($r = 0.55$, $r^2 = 0.31$, $F = 21.9$ and $r = 0.58$, $r^2 = 0.34$, $F = 25.79$, respectively, with $p < 0.0001$, $m = 0.45$ and 0.42 respectively, $N = 52$) (figures 10–11).

There is also a positive correlation between ln-transformed egg capsules length and width ($r = 0.81$, $r^2 = 0.66$, $p < 0.0001$, $m = 0.71$, $F = 96.45$, $N = 52$) (figure 12). The mean number of embryos per egg capsule is 323 (81–448, SD = 76, N [illegible] = 52, N [illegible] = 208). The ln-transformed mean number of embryos per egg





Figures 6–7. *Crepidula argentina.* **6.** Developing female gonad of an 11.8 mm long individual. Scale bar = 200 μm. **7.** Oocytes in different degree of development, previtellogenic (pv) and vitellogenic (vt) in a female of 17.6 mm of shell length. Scale bar = 70 μm.

capsule is also correlated with female length ($r = 0.45$, $r^2 = 0.2$, $p < 0.01$, $m = 0.78$, $F = 12.87$, $N = 52$) (figure 13). The relation between ln-transformed egg capsule size and ln-transformed mean number of embryos contained was also studied (with egg capsule width: $r = 0.62$, $r^2 = 0.39$, $p < 0.000$ $m = 0.13$, $F = 32.14$; with egg capsule length: $r = 0.66$, $r^2 = 0.44$, $p < 0.0001$, $m = 1.57$, $F = 39.12$, $N = 52$)

The ln-transformed mean number of embryos per brood is 5600 (SD = 3300, N = 51) and is correlated with the ln-transformed female shell length ($r = 0.37$, $r^2 = 0.14$, $p < 0.005$, $m = 0.46$, $F = 1.34$). No correlation was found between the ln-transformed female shell length and the ln-transformed number of capsules per brood. As the F value indicates, all slopes of the regressions were different from zero.

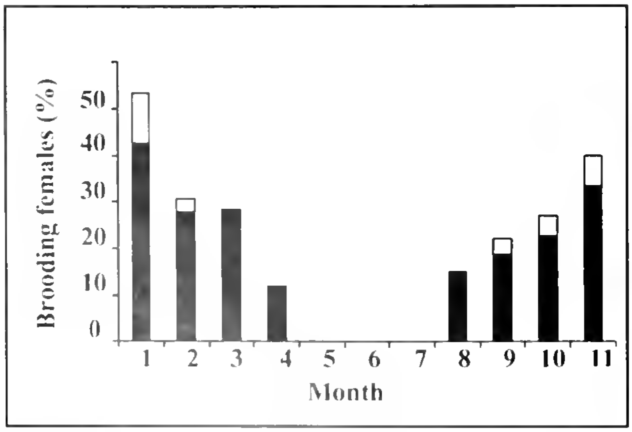


Figure 8. Frequency of brooding females of *Crepidula argentina* from January 1999 to November 1999. The bars represent the percentage of brooding females from the total inspected females within each month. Small females (14–20 mm in shell length) are represented in white, large females (more than 20 mm) are represented in black.

The uncleaved eggs were whitish and approximately spherical with a mean diameter of 170 μm (SD = 9, N = 250). No differences where observed among the five mothers.

Cleavage follows the holoblastic pattern. First and second cleavages are similar, giving rise to four macromeres. All eggs develop. No cannibalism or nurse eggs were observed (Kruskal-Wallis, $p = 0.27$). The development of all embryos in each brood occurs synchronously.

The intracapsular liquid is initially viscous, but becomes less dense toward hatching.

The embryo hatches as a feeding veliger larva. The globular smooth larval shell at hatching measured from live and preserved material was 190–230 μm in length and 195 μm in width (N = 112).

Of the seven egg masses maintained in the aquarium, only one containing late veligers at the time of collection hatched. The colorless, transparent, bilobed velum had a maximum width of 164 μm. Each oval lobe measured 151 μm maximum length. The longest cilia in the pre-

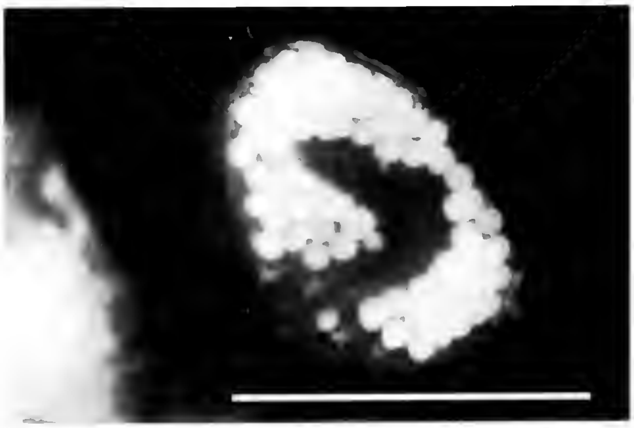
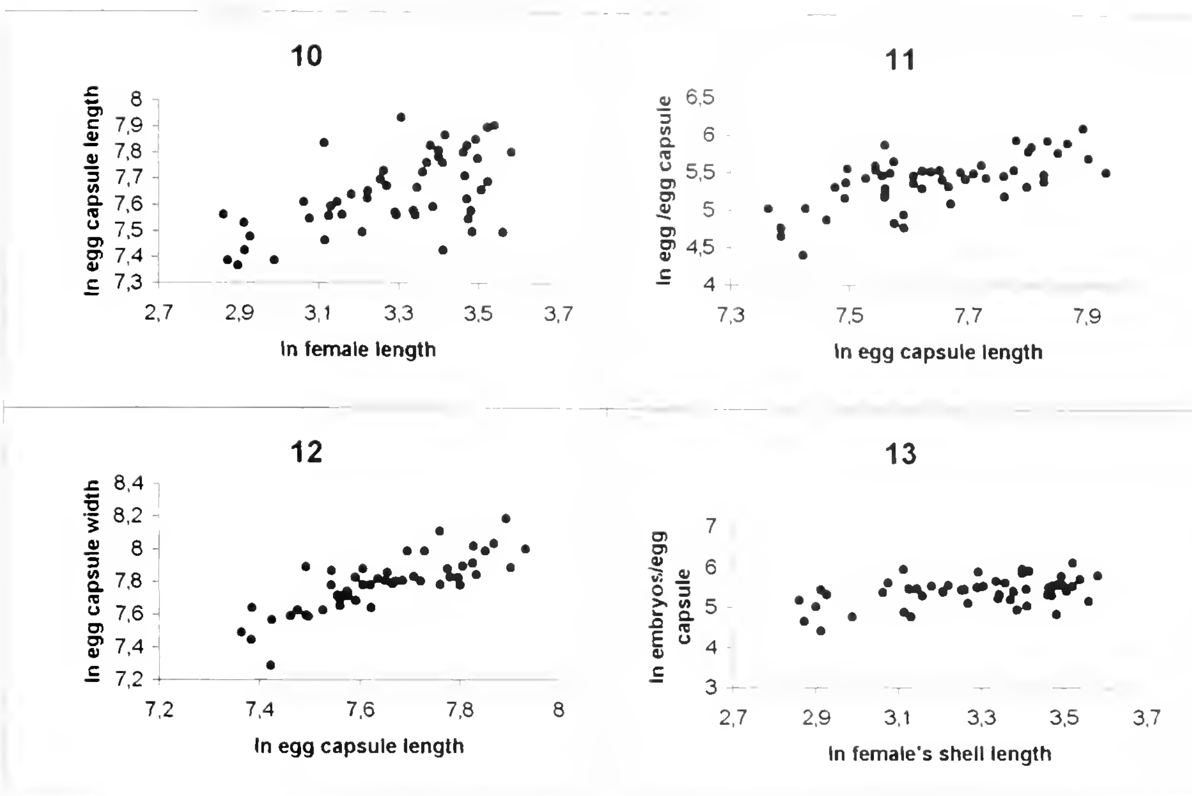


Figure 9. View of an egg capsule of *Crepidula argentina* containing uncleaved eggs. Scale bar = 2 mm.



Figures 10–13. *Crepidula argentina* **10.** Relation between ln female shell length and ln egg capsule length. N = 52. **11.** Relation between ln female shell length and ln egg capsule width. N = 52. **12.** Relation between ln egg capsule length and width. N = 52. **13.** Relation between ln female shell length and ln number of embryos per egg capsule. N = 52. Regression analysis values and their significance are given in the text.

oral ciliary band were 32 µm long. On the anterior part of the velum there is a pair of ciliated tentacles. The triangular ciliated foot possesses an oval operculum, which reaches 67 µm in length and 90 µm in width.

The protoconchs of individuals of 4–6 mm length measured 631 µm mean length (SD = 25, N = 34) (figures 14–15).

DISCUSSION

Crepidula argentina is a protandric hermaphroditic species with complete sex change. The males are already mature at 4 mm shell length. Sex change begins at approximately 9 mm and is completed by 11 mm. Evidence of cytolysis was observed during the whole process of sex change. Furthermore, a fully developed female gonad can be present before the penis is absorbed and the genital papilla developed; such sex change has also been observed in *Crucibulum spinosum* Sowerby, 1824 (Coe, 1938b). At the end of testicular re-absorption the penis disappears, and the oviduct develops (Grimpe and Wegler, 1940).

Crepidula argentina does not form stacks as does *C. fornicata* Linnaeus, 1758. In this latter species, individuals are strongly influenced by each other in their sexual expression (Orton, 1909).

In *C. argentina* a number of mature oocytes is maintained in the gonad even after laying. This suggests that females produce more than one brood per year. This possibility could depend on the duration of brooding.

As in *C. convexa* Say, 1822 (Bandel, 1976), positive correlations were detected in *C. argentina* between female shell length and egg capsule size, mean number of embryos per capsule, and mean capsule length and width: bigger females brood more eggs because the egg capsules are bigger and contain more eggs. However, no correlation was observed between female size and the number of egg capsules per brood.

The South American species *C. convexa* and *C. philippiana* do not show a reproductive resting period (Bandel, 1975; 1976; Gallardo, 1996) while *C. argentina* rests from May to July. Resting periods are also observed in the South American *C. dilatata* Lamarck, 1822, and *C. fecunda* Gallardo, 1979 (Gallardo, 1979). This fact would be related to seasonal water temperature changes. Temperature data in Ramirez *et al.* (1973) and Carreto *et al.* (1998) indicate that bottom temperature at 50 m (where mussel beds with *C. argentina* are located) follows a seasonal cycle with the maximum between February and April (17.5°C) and the minimum between July and September (9.5°C). *Crepidula argentina* does not reproduce in the decreasing temperature period, between May and

Table 1. Characteristics of the reproduction for different *Crepidula* species from South America.

Species	Reference	Number of egg capsules per egg mass	Number of eggs per egg capsule	Uncleaved egg diameter (µm)	Nurse eggs	Hatching stage	Male shell length (mm)	Brooding female shell length (mm)
C. argentina	This study	10–46 (mean = 25, SD = 9)	81–448 (mean = 323, SD 76); all eggs develop.	Mean = 170, SD = 9	No	Veliger larvae; shell length: 190–230 µm	3.95–8.85	14.5–36
C. protea	Hoagland, 1983	26–48 (mean = 31.6, SD = 1.1)	33–120 (mean = 61, SE = 8); all eggs develop.	Not consigned (embryos of 150)	No	Veliger larvae; (size not consigned)	4.6–8	7.3–20
C. dilatata	Gallardo, 1977[1] Chaparro and Paschke, 1990[2]	22–29	308–1016; approximately 15–50 embryos develop	195–263	Yes	Crawling juvenile; shell length: 900–1300 µm[1], 1075–1600 µm[2]	6–26	12–53
C. fecunda	Gallardo, 1977		Mean = 542; all eggs develop.	204–238 (mean = 212)	No	Veliger larvae; shell length: 500 µm	13–49	31–72
C. philippiana	Gallardo, 1977; 1996	16–34	145–431; 1 embryo develops.	144–161	Yes	Crawling juvenile; shell length 2800–3100 µm	6–11	14 and up

July (winter) and presents its maximum reproductive activity between February and March (summer).

Most species of the genus with large females lay eggs with small diameters (Hoagland and Coe, 1982) and this is the case of *C. argentina*. The uncleaved egg diameter is 170 µm with very little variation. There are other species in the genus with a similar egg diameter, like *C. cerithicola* C. B. Adams, 1852, *C. fornicata*, *C. echinus* Broderip, 1834 (Hoagland, 1986) and *C. lingulata* Gould, 1846 (Collin, 2000). *Crepidula argentina* differs from the two first species respectively in that it lacks nurse eggs and produces a different number of egg capsules and it also differs in female size from these two species. *Crepidula argentina* has a mean number of embryos per capsule (323) equivalent to *C. echinus*, a species in which also all eggs develop (Hoagland, 1986). The absence of nurse eggs or cannibalism among sibling embryos accounts for the lack of marked variation in shell length at hatching. Embryonic cannibalism occurs in some other species of the genus but was not observed in *C. argentina*.

The intracapsular liquid is translucent and viscous in recently laid capsules, and becomes less dense as hatching approaches. Because there are no nurse eggs, intracapsular fluid is the only possible extra embryonic food supply. In *C. protea* a sticky matrix in which embryos were embedded, making the embryos difficult to remove from the capsules, has been reported (Hoagland, 1983); this would distinguish *C. protea* from all other *Crepidula* species, including *C. argentina*.

In *C. argentina* the mean number of egg capsules per brood (25) is similar to those of other congeneric species, such as *C. plana* Say, 1822 (Bandel, 1976), *C. cerithicola* and *C. echinus* (Hoagland, 1986).

Crepidula argentina is different from *C. protea* d'Orbigny, 1841, as described by Hoagland (1983) in almost all reproductive aspects examined (table 1).

The individual shell length at metamorphosis in *C. argentina* is around 630 µm in length with remarkably little variation among individuals (SD = 25), which shows a total growth of around 400 µm during planktonic life.

Comparing *Crepidula argentina* with other southern South American species: *C. dilatata* Lamarck, 1822 (Gallardo 1977a) has direct development with nurse eggs. Unlike *C. argentina*, the reproductive period is from May to January with a maximum in July. In *C. dilatata* hatching occurs at the juvenile stage. Males and females have larger shell length ranges than *C. argentina* (table 1). *Crepidula fecunda* (Gallardo, 1979), produces more embryos per brood, its eggs are larger and shell lengths of males and females also exceed adult sizes of *C. argentina* (table 1). *Crepidula philippiana* is easily distinguished from *C. argentina* by presence of nurse eggs; the egg diameter fluctuates between 140–160 µm and only one large juvenile hatches from each capsule (Gallardo 1977b).

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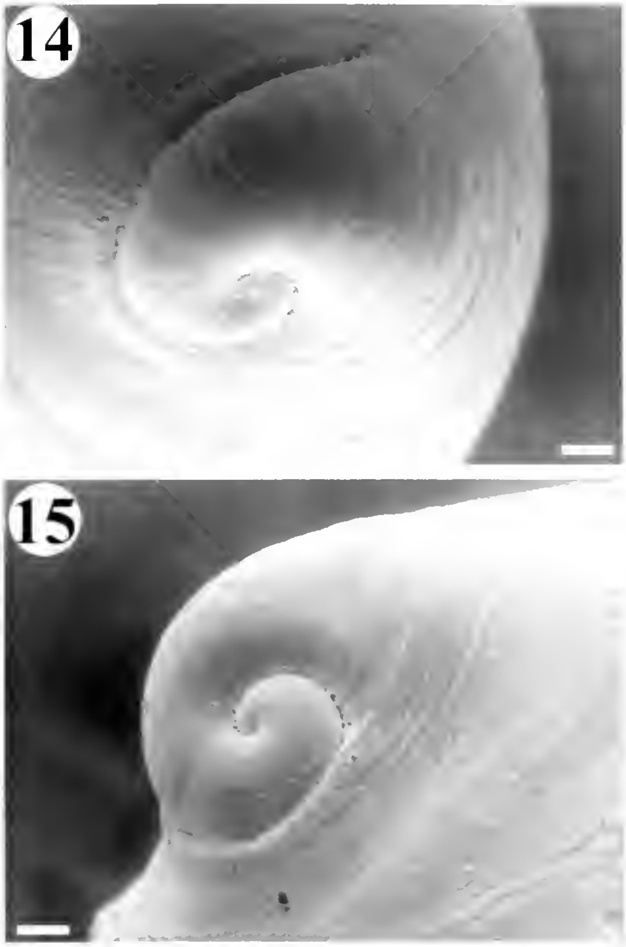

Figures 14–15. *Crepidula argentina* Scanning electron micrographs of the protoconch on 4–6 mm males. Scale bar = 80 μm.

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Revision of the Architectonicidae (Gastropoda: Allogastropoda) from the Miocene Chipola Formation, Oak Grove Sand, and Shoal River Formation of northern Florida, with descriptions of four new species

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ABSTRACT

A revision of the Architectonicidae from the Miocene Chipola Formation, Oak Grove Sand, and Shoal River Formation of northern Florida is presented, along with descriptions of four new species. Two new species are assigned to the genus *Heliacus*, one to the genus *Architectonica* and a fourth to the genus *Granosolarium*.

Additional key words: *Architectonica*, *Heliacus*, *Granosolarium*, Tertiary, Neogene, fossil mollusks.

INTRODUCTION

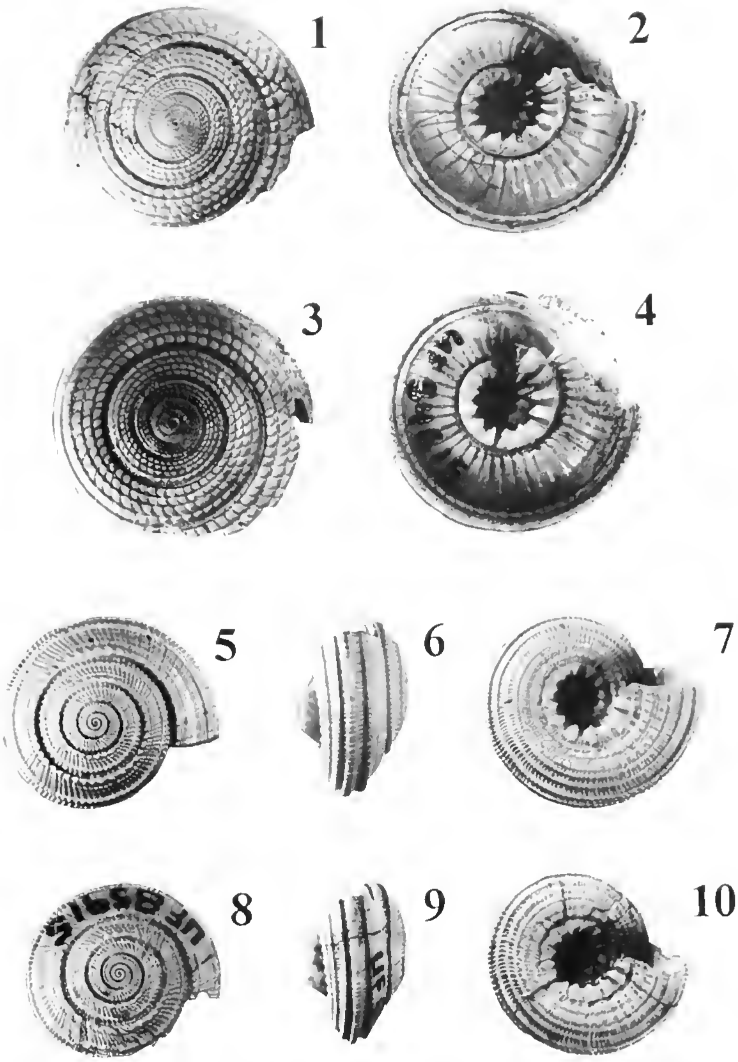
Of the estimated 1100 species of mollusks believed to be represented in northern Florida's Miocene Chipola Formation and Oak Grove Sand deposits only about 640 have been described (Vokes, 1989; 1997). Currently, between 120 and 130 undescribed species of mollusks from the Chipola Formation, Oak Grove Sand, and Shoal River Formation have been discovered by the author in the Invertebrate Paleontology collections at the Florida Museum of Natural History or in private collections. Included among those species that remain to be described are a broad range of specimens representing many different classes and families. This paper is intended to examine four of these new species in the family Architectonicidae.

Bieler (1993) recognized about 140 living species of Architectonicidae. Approximately one third of these extant species are found in the Atlantic and the remainder in the Pacific and Indian oceans (Merrill, 1970). Numerous other species have been reported from fossil deposits (Gardner, 1947; Ladd, 1982; Maury, 1917; Olsson, 1922; Olsson, 1932; Robertson, 1973; Woodring, 1959). Representatives of this family usually have flattened, low-spired shells with heterostrophic protoconchs. Bieler (1993) reported that shells like those of architectonicids have been found in fossil deposits dating back to the Triassic. Among extant groups, Bieler (1993) noted that *Pseudomalaxis* and *Heliacus* appeared first in the Cretaceous while *Architectonica* and other forms appeared in the Eocene. To date, including new forms reported in this paper, a total of eight species of the family are recorded in the Miocene Chipola Formation, Oak Grove Sand, and Shoal River Formation.

Gardner (1947) listed six members of the Architectonicidae from the Alum Bluff Group. Three were morphologically similar to *Architectonica nobilis* Röding, 1798. These include *Architectonica chipolana* (Dall, 1892) from the Chipola River and Tenmile Creek in Calhoun County, Florida, an unnamed subspecies of *Architectonica quadriscriata* (Sowerby, 1850) from the Oak Grove Sand in Florida and Georgia, and *Architectonica quadriseriata waltonensis* Gardner, 1936, from the Shoal River Formation in Walton County, Florida. Of the three remaining taxa, two belong to the genus *Architectonica*. They are *Architectonica alvear* Gardner, 1936, from the Oak Grove Sand and *Architectonica verecunda* Gardner, 1936, from the Shoal River Formation. The third species belongs to the subfamily Heliacinae and was tentatively identified by Gardner (1947), from two "very young" specimens, as *Architectonica bisulcata* (d'Orbigny, 1842).

In this paper we look at four new members of the family Architectonicidae from the Chipola Formation. One is an uncommon species belonging to the genus *Architectonica* that has been collected from only two localities along Tenmile Creek. Two of the remaining species belong to the genus *Heliacus*. Of these, one is fairly common and is well represented in Chipola deposits. This species is most similar to the "very young" specimens of *A. bisulcata* reported by Gardner (1947). The second species of *Heliacus* is extremely rare and is known only from the holotype. The last representative belongs to the genus *Granosolarium*. It is also very rare and is represented by two specimens collected from one locality along Tenmile Creek.

The author also examined seven specimens of the subspecies of *Architectonica quadriseriata* reported by Gardner (1947) from the Oak Grove Sand, in order to



Figures 1–10. New species of Miocene Architectonicidae. **1–4.** *Architectonica gemmosa* new species. **1, 2.** Holotype UF 93992, maximum height 11.8 mm, maximum width 23.5 mm. **3, 4.** Paratype A, UF 84615, maximum height 9.2 mm, maximum width 18.1 mm. **5–10.** *Heliacus* (*Torinista*) *calhounensis* new species. **5, 6, 7.** Holotype, UF 93991, maximum height 8.0 mm, maximum width 15.0 mm. **8, 9, 10.** Paratype A, UF 85915; maximum height 7.2 mm, maximum width 13.7 mm.

determine its taxonomic status. Six of these specimens are the material originally studied by Gardner (deposited at the National Museum of Natural History), while one is from the private collection of Greta and Andy Murray, Bradenton, Florida.

SYSTEMATICS

Superfamily Architectonicoidea Gray, 1850
Family Architectonicidae Gray, 1850
Genus *Architectonica* Röding, 1798

Architectonica Röding, 1798: 78. Type species *Trochus perspectivus* Linnaeus, 1758, by subsequent designation of Gray, 1847.

Architectonica gemmosa new species
(Figures 1–4)

Description: Shell size moderate, low-spired, cone-shaped. Protoconch smooth, maximum diameter 0.94–1.03 mm, with 1.5 whorls. Early half protoconch whorl depressed. Anal keel present. Teleoconch whorls 7, slightly convex, separated by deep, narrow suture. Each teleoconch whorl with 4 prominently sculptured, beaded spiral cords of equal size. Base of sutural groove formed by cord running along peripheral margin of body whorl. Umbilicus moderately wide, outlined by wide, denticulate spiral surrounded by deep, spiral groove. Straight, axial grooves radiate out from spiral groove and cross over wide, fairly smooth band, which, in some specimens, bears faint spiral threads. Two prominent,

raised spiral cords, separated by spiral groove, present at periphery of basal whorl. Innermost cord with well-developed, beaded sculpture. Outermost cord with less distinct sculpturing. In most instances, axial grooves radiating from spiral groove do not join beaded spiral cord on periphery. Shape of aperture unknown as it is badly damaged on all specimens examined.

Holotype: UF 93992, height 11.8 mm, width 23.5 mm.

Paratypes: Paratype A: UF 84615, height 9.2 mm, width 18.1 mm, from type locality; UF 93993–94000, 8 paratypes, Chipola Formation, north bank of Tenmile Creek at powerline crossing about 1 mile west-northwest of mouth of creek at "Bailey's Ferry" (SE 1/4 Sec. 12, T1N, R10W), Calhoun County, Florida (Tulane University locality TU 830).

Type locality: Chipola Formation, Tenmile Creek, about 1.25 miles west of Chipola River (SE 1/4 Sec. 12, T1N, R10W), Calhoun County, Florida (Tulane University locality TU 951).

Distribution: A decade of collecting *Architectonica* from numerous Chipola Formation sites and the examination of hundreds of specimens of *Architectonica* at the Florida Museum of Natural History indicates that *A. gemmosa* is an uncommon species that is exclusively associated with the ancient reef environment that existed along Tenmile Creek in Calhoun County, Florida.

Etymology: Alludes to the species rarity and beautiful sculpture.

Discussion: A number of investigators have noted that living architectonicids have a long-lived veliger stage resulting in a broad geographical range for the adults (Bieler, 1993; Merrill, 1970; Scheltema, 1979). By comparing modern and fossil forms of Atlantic Architectonicidae, Scheltema (1979) was able to demonstrate that the veliger stage of Miocene members of this family also underwent extensive migrations. Hence, in order to make sure the newly discovered Chipola species had not already been described from other Miocene and Pliocene deposits worldwide, specimens were compared with those reported in the literature from a wide range of locations including Europe, the Mediterranean, West Africa, Caribbean, South and Central America, Pacific Ocean, as well as other locations in North America.

Architectonica gemmosa bears some similarities to *Architectonica alvear* Gardner,1936, from the Oak Grove Sand, but *A. alvear* does not have well developed scale-like spiral cords on its dorsal surface and the rugose spiral cord that surrounds the umbilical carina in *A. alvear* is absent in *A. gemmosa*. The only other fossil species that bears any resemblance to *A. gemmosa* is *Architectonica nobilis karsteni* Rutsch, 1934, which was described from Miocene deposits in Venezuela (Rutsch, 1934), central Chile (Frassinetti and Covacevich, 1981) and southwestern Ecuador (Marks, 1951). Woodring (1959) also recorded this latter species from the Pliocene Chagres Sandstone of Panama. However, *A. nobilis karsteni* does not have well developed scale-like spiral cords on its dorsal surface, its umbilical margin is less denticulate, and both peripheral cords on the ventral surface are smooth.

A cursory examination of the "*Architectonica quadrisceriata* ssp." of Gardner (1947) from the Oak Grove Sand and Georgia revealed that it represents *Architectonica chipolana* (Dall, 1892) and should no longer be considered an undescribed subspecies of *Architectonica quadrisceriata*.

Genus *Heliacus* d'Orbigny, 1842

Heliacus d'Orbigny, 1842: 68; introduced as "division" of *Solarium* [= *Architectonica*]. Type species: *Solarium herberti* Deshayes, 1830 [= *Heliacus cylindricus* (Gmelin, 1791)], by monotypy, under the incorrect secondary spelling "heberti".

Subgenus *Torinista* Iredale, 1936

Torinista Iredale, 1936: 327. Type species: *Torinista popula* Iredale, 1936 = *Solarium implexum* Mighels, 1845, by original designation.

Heliacus (Torinista) calhounensis new species
(Figures 5–10)

Description: Shell small, depressed, with flattened apex. Protoconch smooth, sunken, maximum diameter 0.53 mm, with about 1.5 whorls. Anal keel present. Teleoconch whorls 5.5, separated by deep suture. Single row of well-developed, raised spiral cords runs along whorls just above and below suture. Two less distinct spiral cords lie between raised ones. Spiral cords crossed by strong radial ribs that give them beaded appearance. Five prominent, elevated, spiral cords extend from outer edge of last whorl to region halfway across base of shell. First 3 cords keel-like with second one being largest. Remaining 2 cords less distinct. Three prominently sculptured cords, two outermost beaded, innermost strongly denticulate, surround wide umbilicus. All raised spiral cords along side and base intersected by well-developed axial ribs. Aperture circular; outer lip crenulate.

Holotype: UF 93991, maximum height 8.0 mm, maximum width 15.0 mm.

Paratypes: Paratype A: UF 85915, maximum height 7.2 mm, maximum width 13.7 mm, Chipola Formation, Tenmile Creek, about 1.25 miles west of Chipola River (SE 1/4 Sec. 12, T1N, R10W), Calhoun County, Florida (Tulane University locality TU 998); paratype lot UF 95074, 2 shells, Chipola Formation, Tenmile Creek, about 1.25 miles west of Chipola River (SE 1/4 Sec. 12, T1N, R10W), Calhoun County, Florida (Tulane University locality TU 951); paratype lot UF 91794, 3 shells, Chipola Formation, east bank of Chipola River, about 1,000 feet above Fourmile Creek (SW 1/4 Sec. 29, T1N, R9W), Calhoun County, Florida (Tulane University Lo-

cality TU 555); paratype lot UF 84566, 6 shells, Chipola Formation, Tenmile Creek, at powerline crossing about one mile west of Chipola River (SE 1/4 Sec. 12, T1N, R10W), Calhoun County, Florida (Tulane University Locality TU 830); paratype lot UF 95075, 1 shell, Chipola Formation, Tenmile Creek, about 1 1/4 miles west of Chipola River (SE 1/4 Sec. 12, T1N, R10W), Calhoun County, Florida (Tulane University Locality TU 951); paratype lot UF 101100, 1 shell, Chipola Formation, Tenmile Creek, about 1.25 miles west of Chipola River (SE 1/4 Sec. 12 T1N, R10W), Calhoun County, Florida (Tulane University Locality TU 998).

Type locality: Chipola Formation, Tenmile Creek, about 1.25 miles west of Chipola River (SE 1/4 Sec. 12, T1N, R10W), Calhoun County, Florida (Tulane University locality TU 951).

Distribution: *Heliacus calhounensis* is a fairly common species that is widely distributed throughout fossil deposits found along Tenmile Creek, Farley Creek, and the Chipola River. Thus far there are no reports of it being collected from Oak Grove Sand.

Etymology: Named after Calhoun County, Florida.

Discussion: As a small member of the family Architectonicidae, *Heliacus* has a more reticulate and stronger sculpture than those individuals belonging to the genus *Architectonica* (Keen, 1971). Most *Heliacus* are 20 mm or less in size and extant individuals of this genera are identified by their distinctive spiral operculum which is a horny, pagoda-like structure with a fringed edge (Keen, 1971). Since the opercula are not preserved as fossils, other characteristics are used to differentiate fossil species. These features include the type sculpturing on the dorsal and ventral surfaces of the teleoconch whorls, the presence or absence of an anal keel, the widths of the protoconch and umbilicus, and the type of sculpturing surrounding the umbilicus.

Currently, Bieler (1993) has identified six subgenera that belong to the genus *Heliacus*. Based upon external morphological features, the two new species of *Heliacus* described in this paper have been assigned to the subgenus *Torinista*. According to Bieler (1993), this subgeneric group possesses disk-shaped teleoconch whorls with approximately five noded, spiral ribs. On the side of the body whorl, they also have strong lower peripheral and infraperipheral ribs surrounding one or two additional strong ribs.

Heliacus calhounensis was misidentified as *Architectonica* (*Pseudotorinia*) *bisulcata* d'Orbigny, 1853) by Gardner (1947), as she only had access to two very young specimens. An examination of several juvenile *H. calhounensis* by this investigator (two to three millimeters in diameter) revealed that the young do bear a slight resemblance to the latter species. However, the juveniles of *H. calhounensis* possess more heavily beaded spiral cords around the umbilicus and have fewer and less pronounced beaded spiral threads on the dorsal surface.

A number of species of *Heliacus* which appear to belong to the subgenus *Torinista* have been reported from different fossil deposits (Gardner,1948; Jung, 1969; Ladd, 1982; Mansfield, 1930; Maury, 1917; Olsson, 1964; Petuch, 1994; Pilsbry, 1922; Woodring, 1959). *Heliacus calhounensis* is most similar to *Solarium stonemanae* Maury, 1917 from the Miocene Gatun Formation of Panama (Woodring, 1959) and the Pliocene deposits of the Cercado Formation in the Dominican Republic (Maury, 1917). However, it differs from this species by the presence of keel-like spiral cords along its periphery, faint spiral cords on the dorsal surface, and weaker radial growth lines.

Among extant species *H. calhounensis* is closely related to *H. planispira* (Pilsbry and Lowe, 1932), but is not flat-topped, has a more well developed suture between the dorsal whorls, and a wider, more denticulate cord surrounding the umbilicus.

Heliacus (*Torinista*) *compactus* new species
(Figures 11–13)

Description: Small, depressed, cone-shaped shell with angular periphery. Protoconch smooth, maximum diameter 0.64 mm, with 1.3 whorls. First 0.5 protoconch whorl sunken. Anal keel present. Five teleconch whorls, first 2.5 whorls flattened, the remainder angled at 45° toward periphery. Suture distinct, narrow. Five axial rows of irregular-shaped beaded cords present on surface of whorls. These include two medium-size beaded cords adjacent to the suture followed by a single, narrow axial row of beads, a wide trapezoid scale-like cord, and a double row of narrow beads at the periphery. An angled periphery is formed by 2 peripheral ribs. The area between the peripheral ribs sculptured with trapezoid, scale-like beads. Five prominently beaded cords surround deep umbilicus, the innermost one strongly denticulate. Aperture oval.

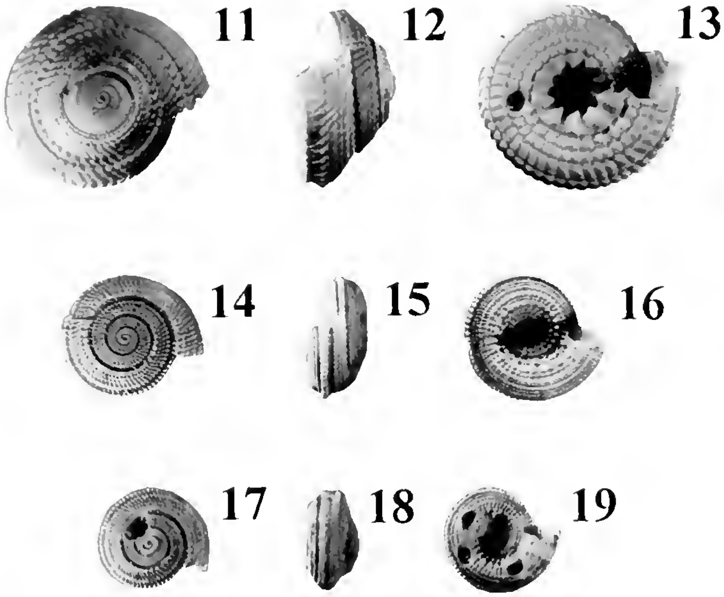
Holotype: UF 93987, maximum height 6.8 mm, maximum width 11.3 mm.

Type locality: Chipola Formation,Tenmile Creek about 1.75 miles west of Chipola River (NE 1/4 Sec. 12, T1N, R10W), Calhoun County, Florida (Tulane University locality TU 546; = USGS 2212, "one mile west of Bailey's Ferry").

Distribution: *H. compactus* is a very rare species that is only known from the type locality.

Etymology: Alludes to tightly spiraled sculpture on the body whorls.

Discussion: *Heliacus compactus* is a unique member of this genus and does not bear a strong resemblance to any other species from the Chipola Formation, Oak Grove Sand, and Shoal River Formation. From the fossil record *Architectonica* (*Pseudotorinia*) *guppyi* Jung, 1969, and *Architectonica* (*Architectonica*) *fusicava* McNeil,1984 are the only species which exhibit any similarities to *H. compactus*. The former species is known



Figures 11–19. New species of Miocene Architectonicidae. **11–13.** *Heliacus (Torinista) compactus* new species, Holotype, UF 93987; maximum height 6.8 mm, maximum width 11.3 mm. **14–19.** *Granosolarium floridanum* new species. **14, 15, 16.** Holotype, UF 96324; maximum height 2.0 mm, maximum width 6.3 mm. **17, 18, 19.** Paratype A, UF 96325; maximum height 1.8 mm, maximum width 4.5 mm.

from several small specimens that were found in the Pliocene deposits of Matura Bay in Trinidad (Jung, 1969). Both *H. compactus* and *A. guppyi* are low spired shells with with submerged protoconchs that possess five beaded axial cords on the teleconch whorls and have an angulate periphery. However, *H. compactus* is much larger, has a much more flattened apex, and the sculpturing on its dorsal and ventral surfaces differ considerably from *A. guppyi*. *Architectonica fuscicava* comes from Oligocene Mint Spring Formation and the Byram Formation of Mississippi (McNeil and Dockery, 1984) and is probably the ancestor to the Miocene species. *Heliacus compactus* is about the same size and possesses the same general shape as *A. fuscicava*, but the spiral beaded sculpturing on both the dorsal and ventral surface of *H compactus* is much larger than the beaded sculpturing on *A. fuscicava*

Genus *Granosolarium* Sacco, 1892

Granosolarium Sacco, 1892: 59. Type species: *Solarium millegranum* Lamarck, 1822, by original designation.

Granosolarium floridanum new species
(figures 14–19)

Description: Shell small, trapezoid-shaped with beaded spiral sculpture and sharp, beaded peripheral keel. Protoconch smooth, depressed, maximum diameter 0.54–0.65 mm, distinctly heterostrophic, with 2 whorls. Anal keel present. Teleoconch 3.5 whorls, deep suture between each whorl. Opposing sides of each teleoconch whorl with prominent beaded cord adjacent to suture. Between the prominent beaded spiral cords on each whorl, are three, less distinct, tile-like cords. Umbilicus very wide. Lower inner peripheral margin of body whorl extends down into umbilicus, which bears two parallel, strongly beaded carinae, that spiral toward the inner apex of shell (into umbilicus). Remainder of ventral surface with six beaded spiral cords of irregular size. Aperture oval.

Holotype: UF 96324, maximum height 2.0 mm, maximum width 6.3 mm.

Other type material: Paratype A, UF 96325, maximum height 1.8 mm, maximum width 4.5 mm, from type locality.

Type locality: Chipola Formation, north bank of Tenmile Creek at powerline crossing about 1 mile west-northwest of mouth of creek at "Bailey's Ferry" (SE 1/4 Sec. 12, T1N, R10W), Calhoun County, Florida (Tulane University locality TU 830).

Distribution: This appears to be a very rare species that has thus far been collected only from the ancient reef environment of the type locality.

Etymology: Named after the state of Florida.

Discussion: *Granosolarium floridanum* readily stands out from the rest of the Architectonicidae found in the Chipola Formation. In general, it has the overall body form of the genus *Architectonica* but differs from this group by its broad umbilicus and prominent peripheral keel. Bieler (1993) assigned members of the Architectonicidae with these characteristics to the genus *Granosolarium*.

Granosolarium floridanum bears some similarity to *Architectonica (Pseudotorinia) eupreпes* Woodring, 1928, from the Pliocene of Jamaica. Both are about the same size, but *G. floridanum* is more dorso-ventrally compressed, the sutures on the dorsal surface are more distinct, and it possesses fewer beaded spiral cords around the umbilicus. *Granosolarium floridanum* is somewhat similar to *Granosolarium asperum* (Hinds, 1844) an extant form which is listed by Bieler (1993) from a number of diverse locations including Australia, New Zealand, Indonesia, and West Africa.

Granosolarium asperum has also been reported from the middle Miocene fossil deposits of Australia (Garrard, 1961) and from the Pleistocene deposits of New Hebrides (Ladd, 1982). However, *G. floridanum* differs from *G. asperum* in that it possesses tile-like sculpturing on its dorsal surface and paired, strongly beaded, carinae around the outer margin of the umbilicus.

Four species of *Granosolarium* have been described from Eocene deposits in the New World, but they are all larger and have finer dorsal and ventral sculptural features than those in *G. floridanum*. Two were collected from the Moodys Branch Formation in Louisiana and described by Palmer (1947). They are *Architectonica (Granosolarium) ornata jacksonia* Palmer, 1947, and *Architectonica (Granosolarium) meekana subsplendida* Palmer, 1947. *Architectonica aldrichi* (Dall, 1892) was collected from the Lower Claiborne of Mississippi and *Architectonica elaborata* was obtained from the lower Claiborne and Gosport Sand of Alabama (Palmer, 1937).

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On the publication date, authorship, and type species of *Umbraculum* and *Tylodina* (Gastropoda: Opisthobranchia: Tylodinoidea)

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ABSTRACT

The genus name *Umbraculum* Schumacher, 1817 is a senior synonym of *Umbrella* Lamarck, 1819, *Gastroplax* de Blainville, 1819, *Ombrella* de Férussac, 1821, *Umbella* delle Chiaje, 1831, and *Operculatum* Mörch, 1852. Other names previously introduced for this genus are not available in the meaning of the International Code of Zoological Nomenclature. Several authors have alternatively considered *Patella sinica* Gmelin, 1791, or *Patella umbracula* Lightfoot, 1786, to be the type species of *Umbraculum*. However, since none of these species was listed in the original description of this genus, they are not eligible to be the type species. *Acardo umbella* Lamarck, 1801 [= *Umbraculum umbraculum* (Lightfoot, 1786)] is here selected to be the type species of *Umbraculum*. In addition, a valid designation of type species for *Umbrella*, *Ombrella*, and *Operculatum* could not be found in the literature; *Umbrella indica* Lamarck, 1819, is here selected to be the type species of these genera. Thus, these three names become objective synonyms. The genus name *Tylodina* Rafinesque, 1814, type species *Tylodina punctulata* Rafinesque, 1814 [= *Tylodina perversa* (Gmelin, 1791)], by monotypy, was published in 1814 and not in 1819.

Additional key words: historical revision, nomenclature, type-species designation.

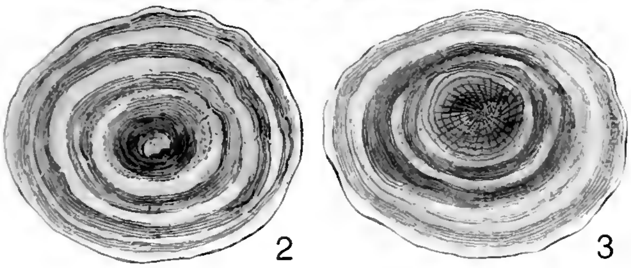
INTRODUCTION

The genera *Umbraculum* and *Tylodina* include relatively well-known opisthobranch mollusks, recently redescribed by Willan (1987). They appear to be closely related opisthobranchs, classified within the Umbraculoidea Dall, 1889 (Willan, 1987), or more correctly Tylodinoidea J. E. Gray, 1847 (Willan, 1998). Both taxa are characterized by a dorsal, external shell, resembling an umbrella or Chinese hat. Members of *Umbraculum* and *Tylodina* have been known since the late 1700s, but so far only a few species belonging to these genera have been described. According to Burn (1959) there is only one valid species of *Umbraculum* distributed throughout all tropical and subtropical seas, whereas Thompson (1970) distinguished an Atlantic and an Indo-Pacific species, and Marcus (1985) recognized a third species from the Caribbean Sea. Thompson (1970) suggested that all species of *Tylodina* should be merged into a single one, whereas Willan (1987) considered that this genus contains five valid species. *Umbraculum* and *Tylodina* are also known from the fossil record (Valdés and Lozouet, 2000), and several fossil species of *Umbraculum* have been described. Another related genus is *Anidolyta* Willan, 1987, type species *Anidolyta duebeni* Lovén, 1846, which contains less than five valid species (Warén and di Paco, 1997). Two other genera previously assigned to the Tylodinoidea are *Bertinia* Jousseaume, 1883 and *Spiricella* Rang and Des Moulins, 1828 (Pruvot-Fol, 1954; Willan, 1987). *Bertinia* has been recently transferred to the Patellogastropoda (see Kase and Valdés, 1997), and the systematic position of *Spiricella* remains uncertain, but this latter genus probably represents an opisthobranch mollusk (Valdés and Lozouet, 2000).

A review of the literature shows a large degree of disagreement among different authors regarding the valid name and type species of *Umbraculum* and the date of publication of *Tylodina*. The present paper attempts to determine the valid name, exact date of publication, and type species of these two genera and their synonyms. In order to reconstruct the nomenclatural history of *Umbraculum* and *Tylodina*, this paper reviews the original descriptions of these two genera as well as other related literature.

DISCUSSION

Species of Tylodinoidea were named and described for the first time in several classic papers. These animals, known only from the shell, were thought to be patellogastropods (Gmelin, 1791; Bosc, 1802), or a single valve separated from species of the bivalve genus *Acardo* Commerçon *in* Bruguière, 1789 (see Lamarck, 1801;



Figures 1–3. Classic illustrations of *Umbraculum*. **1.** Martini's (1769) 'Parasol Chinois'. **2.** Dorsal view of Chemnitz's (1788) 'Umbella Chinensis'. **3.** Ventral view of Chemnitz's (1788) 'Umbella Chinensis'. All illustrations originally in color.

Most of the classic descriptions of species and genera of Tylodinoidea are not consistently binominal, and therefore most of the names introduced at that time are not available (International Commission on Zoological Nomenclature, 1999: Article 11). Dávila (1767) and Martini (1769) described species of *Umbraculum* for the first time, under the names 'Lepas Umbella Chinensis' and 'Parasol Chinois' (Figure 1) respectively. Chemnitz (1788) compiled early descriptions of Tylodinoidea under the name 'Umbella Chinensis' (Figures 2–3), including 'Operculatum laeve' of Linnaeus (1753), Favart d'Herbigny's (1775) 'Parasol Chinois', *Patella parva* Da Costa, 1778 and de Favanne's (1780; 1784) 'Parasol Chinois'. All these references appear to be species of *Umbraculum* except Da Costa's (1778) *Patella parva*, which is a synonym of the patellogastropod *Tectura virginea* (Müller, 1776). The works of Martini (1769) and Chemnitz (1788) have been placed in the Official Index of Rejected and Invalid Works in Zoological Nomenclature.

Lightfoot (1786) introduced for the first time a binominal name for a species of *Umbraculum*, *Patella umbracula* Lightfoot, 1786. Curiously, *Patella umbracula* Lightfoot, 1786 was not listed by Sherborn (1902), who only alluded to Gmelin's (1791) descriptions of species of Tylodinoidea: *Patella sinica* for *Umbraculum*, and *Patella perversa* for *Tylodina*. Dance (1962) revised Lightfoot's (1786) work, which meets the criteria of publication of the Code (International Commission on Zoological Nomenclature, 1999: Article 8).

The Valid Name and Type Species of *Umbraculum*

The vernacular name 'Umbella' was used in classic literature to designate species of Tylodinoidea (Dávila, 1767; Chemnitz, 1788). Lamarck (1801) described a new species of mollusk, *Acardo umbella* Lamarck, 1801, based on vernacular references by Dávila (1767) and Martini (1769). These two references are descriptions and drawings of shells of *Umbraculum*, and therefore the species *Acardo umbella* Lamarck, 1801, belongs to this genus. One of these references, 'Umbella Chinensis' of Chemnitz (1788), was published in binominal form by Lamarck (1801) as *Umbella chinensis*. Apparently, Lamarck (1801) was the first author to name *Umbella* in the binominal form, but he introduced this name in the synonymy of *Acardo*, therefore rendering it unavailable (International Commission on Zoological Nomenclature, 1999: Article 11.6). Gray (1847) considered that 'Umbella' was originally and validly introduced by Chemnitz, and selected 'Patella umbellata' to be the type species of this genus.

Lamarck (1801) believed that *Acardo* represented a bivalve mollusk, and that *Umbella chinensis* was described by Chemnitz (1788) based on a single valve of his new species *Acardo umbella* Lamarck, 1801. However, a re-examination of the description and illustrations by Chemnitz (1788: 341, pl. 169, figs 1645–1646), clearly shows that 'Umbella Chinensis' is a species of Tylodinoidea (Figures 2–3). This was recognized by Schumacher (1817) and Pilsbry (1895–96). The genus *Acardo*, type species *Acardo crustularius* Commerçon *in* Bruguière, 1789, was later found to be an epiphysis of a whale, not a mollusk (Deshayes, 1830; Gray, 1847).

Apparently, Lamarck (1812) recognized that his *Acardo umbella* was not a valve of *Acardo*, but a different genus of gastropod mollusks, and introduced for the first time the genus name 'Ombrelle', with a very short description and no specific names associated with it. However, Lamarck's (1812) work is not consistently binominal and does not meet the criteria of availability of the Code (International Commission on Zoological Nomenclature, 1999: Article 11). Years later, Lamarck (1819) again used the name 'Ombrelle' for this genus of gastropod mollusks, this time also Latinized as *Umbrella*. At the same time Lamarck (1819) described two new species, *Umbrella indica* Lamarck, 1819, and *Umbrella mediterranea* Lamarck, 1819, and regarded *Gastroplax* de Blainville, 1819, as a synonym of *Umbrella*. De Blainville (1819) based *Gastroplax* on a single species, 'Patella ombracula Chemnitz', with valid binominal name *Umbraculum umbraculum* (Lightfoot, 1786), of which it is the type species by monotypy. Lamarck's (1819) paper is consistently binominal, and Sherborn (1925) and Neave (1939) regarded it as the first valid introduction of the genus name *Umbrella*. In addition, Lamarck (1819) described for the first time the soft parts of a representative of this genus, a task later completed by Moquin-Tandon (1870). In the following years, and during most of the 19th Century, the genus name *Umbrella* gained

universal acceptance. Examples of usage of this name are the papers by Menke (1828), Rang (1829), Deshayes (1830), Philippi (1836), Sowerby (1839), Cantraine (1841), Herrmannsen (1846–49), Souleyet (1852), Fischer (1880–87), Vayssière (1885) and Locard (1892). Most of these authors considered Lamarck's (1812) work as the first valid description of this genus, and subsequently Herrmannsen (1846–49) [1849] selected 'Patella umbrella Chemn.' as type species of the genus. The first valid introduction of the genus *Umbrella* is Lamarck's (1819). 'Patella umbrella Chemn.' is not a valid species and was not originally listed in the description of the genus. Therefore, Herrmannsen's (1846–49) [1849] is not a valid type-species selection for *Umbrella*. I have not been able to find in the literature a valid designation of type species for *Umbrella* Lamarck, 1819, thus *Umbrella indica* Lamarck, 1819 [= *Umbraculum umbraculum* (Lightfoot, 1786)] is here selected to be the type species of the genus.

Schumacher (1817) described the genus *Umbraculum* based on references to Martini's (1769) 'Parasol Chinois', de Favanne's (1780; 1784) 'Parasol chinois', Chemnitz's (1788) 'Umbella Chinensis', *Acardo umbella* Lamarck, 1801, *Patella umbellata* Bosc, 1802, and *Acardo orbicularis* Megerle von Mühlfeldt, 1811. Subsequently, Pilsbry (1895–96) [1896] selected *Umbraculum sinicum* (Gmelin, 1791) to be the type species, and at the same time considered that several of the species cited in the original description of *Umbraculum* were synonyms of *U. sinicum*. Other authors (Thompson, 1970; Marcus, 1985; Willan, 1987) considered *Patella umbracula* Lightfoot, 1786, to be the type species of *Umbraculum*. According to the Code (International Commission on Zoological Nomenclature, 1999: Article 67.2), since *Umbraculum sinicum* (Gmelin, 1791) and *Patella umbracula* Lightfoot, 1786, were not included in the original description of *Umbraculum*, neither of these two designations of type species is valid. I have not found in the literature a valid selection of type species for *Umbraculum*; accordingly, *Acardo umbella* Lamarck, 1801, which was included in the original description of *Umbraculum*, is here selected to be the type species of this genus. According to Pilsbry (1895–96), *A. umbella* is a junior synonym of *U. sinicum*, which is also a junior synonym of *U. umbraculum* (see Willan, 1987). There is no question that *Umbraculum* and *Umbrella* were described with the same features, and most authors regarded both names as synonyms (see Willan, 1987).

Pilsbry (1895–96) noticed for the first time that *Umbrella* was validly introduced by Lamarck in 1819, and not in 1812, and therefore that *Umbraculum* was a senior synonym of *Umbrella*. In the following years, all authors followed Pilsbry's opinion, and the genus name *Umbrella* has not been used as valid for more than one hundred years. The latest papers I found using the name *Umbrella* as valid are those by Vayssière (1885) and Locard (1892). Since Pilsbry's (1895–96) paper, the genus name *Umbraculum* has gained universal acceptance and it is now in constant and exclusive use.

Other Synonyms of *Umbraculum*

Some of the vernacular or unavailable genus names introduced for species of *Umbraculum* in the classic papers mentioned above, were later latinized or became available by other means. These names are thus junior synonyms of *Umbraculum*. Férussac (1821), latinized for the first time the name *Ombrella*, based on the French spelling 'Ombrelle', also used by Lamarck (1812; 1819) for *Umbrella*. Delle Chiaje, 1830–31 [1831] again latinized the genus name *Umbella*, this time not in synonymy, and therefore he is the author of the name. Mörch (1852) made available the genus name *Operculatum* for the first time, which is a binominalization of 'Operculatum' Linnaeus, 1753. In the original descriptions of both *Ombrella* and *Operculatum* several species were listed and no type species was designated. I have selected *Umbrella indica* Lamarck, 1819, which is mentioned by Férussac (1821) and Mörch (1852) to be the type species of both genera.

Willan (1987) suggested that *Spiricella* could be a synonym of *Umbraculum*, but this genus is clearly distinct and probably not even a member of the Tylodinoidea (see Valdés and Lozouet, 2000).

The Date of Publication of *Tylodina*

The genus name *Tylodina* was originally and validly introduced by Rafinesque in 1814 and not in 1819, as suggested by some authors (e.g., Pilsbry, 1895–96; Willan, 1987). Several sources (Herrmannsen, 1846–49; Sherborn, 1925; Neave, 1939) already pointed to the work by Rafinesque (1814) as the first valid introduction of the name *Tylodina*.

Pilsbry (1895–96), and subsequently other authors, considered that the genus *Tylodina* was introduced for the first time by Rafinesque (1815), who mentioned the name *Tylodina* without a description. According to Pilsbry (1895–96), *Tylodina* Rafinesque, 1815, is a *nomen nudum*. Later, Rafinesque (1819) published a full description of *Tylodina*, which was regarded by Pilsbry (1895–96) as the valid original description of the genus. However, Rafinesque (1819) mentioned: "Since the 12th and latest issue of my *Journal encyclopédique de la Sicilie* [Rafinesque, 1814] is not in Paris, and it was almost completely destroyed during the two consecutive shipwrecks that I suffered, I am sending you the characters of eleven genera of mollusks and polyps, among the 36 new genera that it contains, begging you to publish them again". It is evident then, that the genus *Tylodina* was actually first described in 1814, and that most copies of the 12th issue of this paper were lost in the mentioned shipwrecks.

I found a copy of Rafinesque's (1814) work at the library of the Muséum national d'Histoire naturelle in Paris, but as Rafinesque commented in 1819, issue 12 (volume 2) is missing. However, there are still copies of that work available in public libraries in the United States. Fitzpatrick (1911) described in detail Rafin-

esque's (1814) work and mentioned the 12th and last issue of volume 2 (pp. 161–196). This issue includes a chapter entitled "Somiologia. Definizioni di 36 nuovi Generi di Animali marini della Sicilia, pp. 161–166" that contains the original description of *Tylodina*. A part of this chapter, including only 11 of the 36 originally described genera, was published again by Rafinesque (1819), repeating the description of *Tylodina*. According to Fitzpatrick (1911) there are full copies of Rafinesque's (1814) work at the Library of the Academy of Natural Sciences of Philadelphia and the Library of the Historical Society of Pennsylvania. Another copy, lacking issue 12 of volume 2, is at the Library of the Congress. There are more copies lacking several issues in other public libraries in the United States. Sherborn (1925) cited Rafinesque's (1814) paper and mentioned the page number with the original description of *Tylodina* (p. 162), so it is very likely that he also saw one of the remaining complete copies. Unfortunately, I had not direct access to any of Rafinesque's (1814) complete copies of this work, which, due to its rarity, are no longer available for loan or reproduction.

Binney and Tryon (1864) compiled the papers by Rafinesque, but they did not include the paper of 1814 on *Tylodina*, only the papers of 1815 and 1819. This was probably the reason why Pilsbry (1895–96) and subsequent authors erroneously determined 1819 as the original publication date of *Tylodina*.

Joannisia di Monterosato, 1884 (type species *Tylodina citrina* Joannis, 1853, by original designation), and *Tylodinella* Mazzarelli, 1897 (type species *Tylodinella trinchesii* Mazzarelli, 1897, by monotypy), are junior synonyms of *Tylodina* (see Willan, 1987). The genus *Parmophorus* de Blainville, 1817 (type species *Parmophorus elongatus* de Blainville, 1817) is a synonym of *Scutus* de Montfort, 1810 (Fissurellidae) and not a synonym of *Tylodina* as suggested by Willan (1987). When introducing this new genus, de Blainville (1817) mentioned that *Parmophorus* is just a translation into Greek of the name *Scutus*.

The type species of *Tylodina*

Rafinesque (1814) introduced the genus *Tylodina* based on a single species, *Tylodina punctulata* Rafinesque, 1814 (described in the same work), which became the type species by monotypy (see Sherborn, 1925). Willan (1987) erroneously stated that Pilsbry (1895–96) selected *Tylodina citrina* Joannis, 1834, to be the type species of *Tylodina* by subsequent designation. The species name *T. citrina* is not mentioned in any of Rafinesque's papers dealing with *Tylodina* (1814; 1815; 1819) and therefore it is not eligible to be the type species. Moreover, Pilsbry (1895–96) did not select a type species for *Tylodina*.

Pilsbry (1895–96) commented that it was uncertain which species of *Tylodina* was known to Rafinesque. Pilsbry (1895–96) considered several valid species of this genus to coexist in the Mediterranean Sea. In light of Willan's (1987) review of *Tylodina* it appears that there is only one valid Mediterranean species, *Tylodina perversa* (Gmelin, 1791), which is most likely a senior synonym of *T. punctulata*.

CONCLUSIONS

After the critical review of the pertinent literature, the valid name, exact date of publication, and type species of the genera *Umbraculum*, *Tylodina*, and their junior synonyms has been determined. In order to clarify the results of this work a summary synonymy is presented here.

Umbraculum Schumacher, 1817: 177–179.

Type species: *Acardo umbella* Lamarck, 1801 [= *Umbraculum umbraculum* (Lightfoot, 1786)], here designated.

- + *Umbrella* Lamarck, 1819: 339–343. Type species: *Umbrella indica* Lamarck, 1819 [= *Umbraculum umbraculum* (Lightfoot, 1786)], here designated.
- + *Gastroplax* de Blainville, 1819: 182. Type species: *Umbraculum umbraculum* (Lightfoot, 1786), by original designation, originally cited as 'Patella ombracula Chemnitz'.
- + *Ombrella* de Férussac, 1821: xxix. Type species: *Umbrella indica* Lamarck, 1819 [= *Umbraculum umbraculum* (Lightfoot, 1786)], here designated
- + *Umbella* Delle Chiaje, 1822–1831 [1831]: 200, 209, 213. Type species: *Umbella mediterranea* (Lamarck, 1819), by monotypy.
- + *Operculatum* Mörch, 1852: 137. Type species: *Umbrella indica* Lamarck, 1819 [= *Umbraculum umbraculum* (Lightfoot, 1786)], here designated.

Tylodina Rafinesque, 1814: 162.

Type species: *Tylodina punctulata* Rafinesque, 1814 [= *Tylodina perversa* (Gmelin, 1791)], by monotypy.

- + *Joannisia* di Monterosato, 1884: 149. Type species: *Tylodina citrina* Joannis, 1853 [= *Tylodina perversa* (Gmelin, 1791)], by original designation.
- + *Tylodinella* Mazzarelli, 1897: 596–600. Type species: *Tylodinella trinchesii* Mazzarelli, 1897 [= *Tylodina perversa* (Gmelin, 1791)], by monotypy.

ACKNOWLEDGMENTS

I am very grateful to Larry Currie and Patricia Shea-Diner, of the Library of the California Academy of Sciences, for their invaluable help in compiling the literature necessary for the completion of this paper.

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Notes

A note on *Lucina multilineata* "Tuomey and Holmes" (Bivalvia: Lucinidae)

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The species name *multilineata* "Tuomey and Holmes" is in current usage for a species of *Parvilucina* that occurs in the Pliocene and Pleistocene of the Carolinas and Florida and in the Recent Fauna of the western Atlantic from the Carolinas to Brazil.

Tuomey and Holmes (1856: 61, pl. 18, figs. 16, 17) identified this species as *Lucina multistriata* Conrad (1844: 307). They did not cite the original description but cited Conrad's later usage (1845[in 1838–61]: 71, pl. 40, fig. 6). Unfortunately, in citing Conrad they misspelled the species name as *multilineata* instead of *multistriata*. As Conrad is not only shown as author of the binomen, both in the text and on the plate caption, but a reference to his work is also given, it is clear that *multilineata* is an incorrect spelling. Holmes (1858: 29, pl. 6, fig. 6) repeated the error, using the same spelling, and crediting authorship to Conrad.

The first person to credit this name to Tuomey and Holmes was Dall (1903: 1384) who recognized that the shell figured by Tuomey and Holmes was distinct from *L. multistriata* Conrad and cited it as *Phacoides* (*Parvilucina*) *multilineata* Tuomey and Holmes. He placed in synonymy the Recent *Phacoides* (*P.*) *crenella* Dall, 1901. Gardner (1944: 79) followed Dall and added the comment that the misspelling by Tuomey and Holmes was a "happy blunder" as the species they figured was not conspecific with *L. multistriata* Conrad. The validity of Dall's action has never been questioned. However, a misspelling of an attributed name has never made such misspelling an available name. In both the current Code (International Commission on Zoological Nomenclature, 1999) and the one just superceded (International Commission on Zoological Nomenclature, 1985), this is addressed in Article 33. Among the many workers who have followed Dall and Gardner in attributing this name to Tuomey and Homes, always incorrectly dated, are Abbott (1974: 459), Bretsky (1976: 263), Rios (1994: 252), and Turgeon *et al.* (1998: 38). Campbell (1993: 28, figure 63), in reporting the species from the Pliocene of Virginia, correctly dated Tuomey and Holmes but listed no synonyms except for a typographical error by Cooke, 1937.

It appears that the earliest available name for the species figured by Tuomey and Holmes and later authors as *Lucina multilineata* Tuomey and Holmes, is *Parvilucina crenella* (Dall, 1901: 825, pl. 39, fig. 2). Dall's original figure is reproduced by Abbott (1974: 458, fig. 5290).

In recent correspondence with Drs. E. V. Coan and L. D. Campbell concerning this note, they have advised that the systematics of *Parvilucina* of both the eastern Pacific and western Atlantic are in need of revision. The comments of both on this short note are acknowledged with appreciation.

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A replacement name for a New Caledonian *Calliostoma* species (Gastropoda: Trochidae)

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As a result of procedural omission during preparation of a recent paper (Marshall, 1995), I overlooked the fact that a specific epithet chosen for a new *Calliostoma* species was already in use by Quinn (1992).

Calliostoma (Benthastelena) kanakorum new name
Calliostoma (Benthastelena) coronatum Marshall, 1995: 409, fig. 49–51, 128, 156. Not *Calliostoma coronatum* Quinn, 1992.

The replacement name is for the indigenous people of New Caledonia and Vanuatu.

LITERATURE CITED

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Quinn, J. F. 1992. New species of *Calliostoma* Swainson, 1840 (Gastropoda: Trochidae), and notes on some poorly known species from the western Atlantic Ocean. The Nautilus 106:77–144

Erratum

In the section "Type material" in Simone *et al.* (2000: 139) we inadvertently printed an incorrect paratype number. The USNM paratype number therein should be 880725, not 2016009 as originally stated.

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Simone, L. R. L., G. Pastorino, P. E. Penchaszadeh. 2000. *Crepidula agentina* (Gastropoda: Calyptraeidae), a new species from the littoral of Argentina. The Nautilus 114:127–148

Book Review

Panamic Province Molluscan Literature: Additions and Changes from 1971 through 2001

Skoglund, C. 2001. Panamic Province molluscan literature: Additions and changes from 1971 through 2001. 1. Bivalvia. 2. Polyplacophora. The Festivus 32 (supplement):i–v+1–119 (Bivalvia); 1–20 (Polyplacophora).

If the concept of "definitive" could be applied in science, Myra Keen's (Keen, 1971) second edition of *Sea Shells from Tropical West America* would be it. Including in excess of 3300 species and spanning 1064 pages, the volume covered exhaustively the Panamic malacofauna (25°N–6°S) as understood in 1971, packing more information per species than what is the norm for books of its kind. It also brought with it a wealth of bibliographic references. But 30 years have now passed and nothing in science is final and conclusive. Thanks to the work of a large number of West Coast malacologists, some of them Keen's own graduate students, many new taxa were discovered, the identity of others reevaluated, geographic ranges and the phylogenetic relationships among mollusks better defined. Through comprehensive research of the literature, Carol Skoglund has endeavored to bring up to date information on Panamic mollusks in a series of papers previously published in the San Diego Shell Club publication *The Festivus* (e.g., Skoglund, 1989; 1991).

The two-section, non-illustrated volume is informative, well researched, and as Keen's book did before it, yields a huge amount of bibliographical references. After all, this is the main proposal of Skoglund's new volume, to provide an update on taxonomic works on Panamic bivalves and chitons published since 1971. But the volume is much more than just a listing of references on Panamic literature. Species are listed according to currently accepted arrangements: the supraspecific taxonomy of the section on bivalves is structured after the superb work by Coan, Scott and Bernard (2000). Changes in taxonomic, nomenclatural, or geographical status in species previously treated in 1971 are denoted by Keen's original species number (but not necessarily in the same sequence), given in a left-indented column before each entry. This system facilitates cross-referencing and is particularly useful when species are moved to another genus or family. New names introduced since 1971, either as new taxa or under new combinations, are indicated by boldface printing. The treatments are uniform, with topics under each specific entry following an established sequence. The work is plenty in annotations, and no deletions or additions are left unexplained. A taxonomic index, much desired in this type of work, is provided; a spot check showed it to be complete and virtually free of typographic or transcription errors. The same is true for the remainder of the volume, and both author Skoglund and *The Festivus* editor Carole Hertz are to be congratulated on the task.

Although I am far from being a specialist on Panamic bivalves and chitons, I am impressed with the profusion of information and the consistency present in Skoglund's work. A similar update on the Panamic gastropods would be most welcome!

The cost within the US is $22 postpaid, overseas $25 (surface) or $30 (air mail). Contact the San Diego Shell Club, c/o 3883 Mt. Blackburn Ave., San Diego, CA 92111, USA, or e-mail Carole Hertz (cmhertz@pacbell.com) for further ordering information.

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Notices

THE 2001 R. T. ABBOTT VISITING CURATORSHIP

The Bailey-Matthews Shell Museum is pleased to invite applications for the 2001 R. T. Abbott Visiting Curatorship.

The Curatorship, established originally in accordance with the wishes of the late Dr. R. T. Abbott, Founding Director of the Shell Museum, is awarded annually to enable malacologists to visit the Museum for a period of a week. Abbott Fellows will be expected, by performing collection-based research, to assist with the curation of portions of the Museum's collection and to provide one evening talk for the general public. The Museum collection consists of marine, freshwater, and terrestrial specimens. A large percentage of our holdings have been catalogued through a computerized database management system. A substantial portion of the time will be available for research in the collection, but field work in southwest Florida can be arranged. The R. T. Abbott Visiting Curatorship is accompanied by a stipend of $1,500.

Interested malacologists are invited to send a copy of their curriculum vitae together with a letter detailing their areas of taxonomic expertise and research objectives, and provide a tentative subject for their talk. Send materials to:

Dr. José H. Leal
The Bailey-Matthews Shell Museum
P. O. Box 1580
Sanibel, FL 33957
jleal@shellmuseum.org

Applications for the 2001 Visiting Curatorship should be sent no later than May 15, 2001. The award will be announced by late June. Questions about the Visiting Curatorship should be sent to the e-mail address above, or by phone at:

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Manuscripts: Each original manuscript and accompanying illustrations should be submitted in triplicate. Text must be typed on one side of 8½ × 11 inch white paper, double spaced throughout (including literature cited, tables and figure captions), with at least 1 inch of margin on all sides. All pages must be numbered consecutively. If printed on a word processor, the right margin should be ragged rather than justified. Authors should follow the recommendations of the *Scientific Style and Format—The CBE Manual for Authors, Editors, and Publishers*, which is available from the Council of Science Editors, Inc., 11250 Roger Bacon Drive, Suite 8, Reston, VA 20190, USA (http://www.cbe.org/cbe). The first mention of a scientific name in the text should be accompanied by the taxonomic authority, including year. Latin names and words to be printed in italics must be underlined; leave other indications to the editor. Metric and Celsius units are to be used.

The sequence of sections should be: title page, abstract page, introduction, materials and methods, results, discussion, acknowledgments, literature cited, tables, figure captions, figures. The title page should include the title, author's name(s) and address(es). The abstract page should contain the title and abstract, which should summarize in 250 words or less the scope, main results and conclusions of the paper. The abstract may be followed by a maximum of 8 key words. All references cited in the text must appear in the literature cited section and vice versa. In the literature cited section, all authors must be fully identified and listed alphabetically. Follow a recent issue of THE NAUTILUS for bibliographic style, noting that journal titles must be unabbreviated. Information on plates and figures should be cited only if not included in the pagination. Tables must be numbered and each placed on a separate sheet. A brief legend must accompany each table. Captions for each group of illustrations should be typed on a separate sheet and include a key to all lettered labeling appearing in that group of illustrations.

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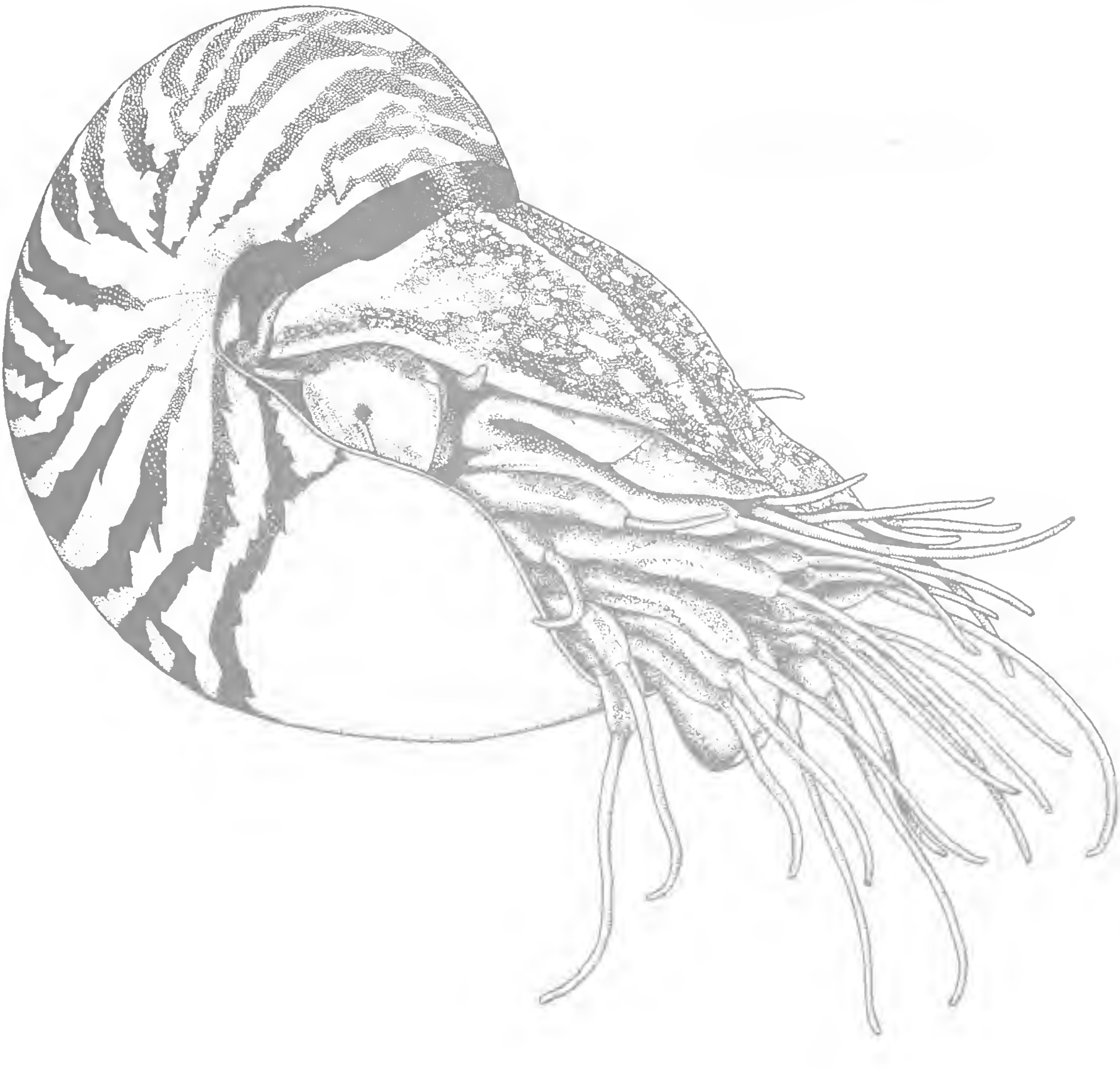

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CONTENTS

Adelphophagy and cannibalism during early development of *Crucibulum auricula* (Gmelin, 1791) (Gastropoda: Calyptraeidae) from the Venezuelan Caribbean

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ABSTRACT

Crucibulum auricula (Gmelin, 1791) was found living attached to rocky substrates at Isla Caribe, Estado Sucre, Venezuela, between 0.5 and 1 m depth. The shell of sexually mature females ranged from 12 to 23 mm in diameter and 6 to 10 mm in height. These females brooded between 4 and 20 egg capsules in the mantle cavity. Each egg capsule had a stalk and the stalks were joined at the point of attachment to the substrate. Each egg capsule measured between 1.6 and 3.5 mm in length (without the stalk) and between 1.0 and 2.8 mm in width. The number of uncleaved eggs per capsule varied between 55 and 305 and measured approximately 220 μm in diameter. All eggs started development and completed the first four divisions, but only 7 ± 4 % (between 3 and 24 eggs per capsule) continued to develop. The remainder was ingested by the embryos as nurse eggs. At the end of this period of adelphophagy, the embryos started to cannibalize each other, after which only 1 to 11 embryos were left in each capsule. Juveniles with a well-developed foot and short cephalic tentacles crawled out of the capsule. Ciliary movement was observed in the region where the velum had been resorbed. The shells are brown, calcified, and measure about 730 μm in length. Both intracapsular feeding strategies, adelphophagy and cannibalism have been previously reported in the family Calyptraeidae. Both strategies are here reported for the first time in a species of the genus *Crucibulum*.

Additional key words: Caenogastropoda, egg capsules, embryonic nutrition, reproduction, nurse eggs, Venezuela

INTRODUCTION

Gastropods of the family Calyptraeidae are characterized by the production of eggs contained in membranous egg capsules that are attached to hard substrates and are brooded between the neck and propodium of the female. The spawn is composed of several sac-shaped egg capsules joined to each other at the base of a stalk. Each sac is composed of a thin membrane and the stalk is a continuation of this membrane. Within genera, some species produce large eggs with large amounts of yolk that hatch as crawling juveniles. Other species produce smaller eggs that hatch as planktonic veliger larvae and others complete intracapsular development by feeding on nurse eggs (Hoagland, 1986).

The genus *Crepidula* Lamarck, 1799, is the best studied in the family. Hoagland (1986) reviewed encapsulation patterns and brooding of about 20 species of *Crepidula* and found that egg diameter is very variable, ranging from 130 to 440 μm. Hatchlings can be planktotrophic veligers, pediveligers or crawling juveniles. Extra-embryonic nutrition, when present, can be in the form of nurse eggs or cannibalism among sibling embryos. Adelphophagy has been reported in at least 7 *Crepidula* species and cannibalism of damaged or abnormal embryos is widespread in the genus (Hoagland, 1986).

The genus *Crucibulum* Schumacher, 1817, is characterized by cap-shaped shells with a complete cup-like support, which is attached by its base or along one side. Abbott (1974) reported 12 American species, 10 in the Pacific from California to Chile and 2 Atlantic species, *Crucibulum auricula* from South Carolina to Texas and West Indies to Brazil and *Crucibulum striatum* Say, 1824 from Nova Scotia to both sides of Florida. Díaz and Puyana (1994) reported 3 species in the Colombian Caribbean, *C. auricula*, *C. marense* Weisbord, 1962, and *C. planum* Schumacher, 1817. Reproduction of species in the genus *Crucibulum* is less known. Coe (1938) studied the sexual phases of *Crucibulum spinosum* Sowerby,

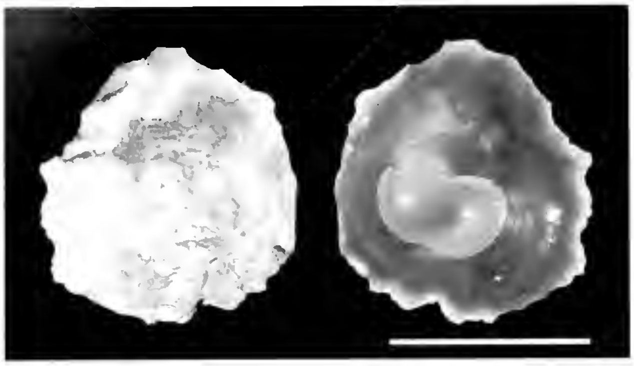


Figure 1. Adult shell of *Crucibulum auricula*. Dorsal and ventral view. Scale bar = 13 mm

1824, from the coast of Southern California. Development of *Crucibulum scutellatum* Wood, 1828, from the Persian Gulf was studied by Thorson (1940). Bandel (1975) described the protoconch of *Crucibulum auricula* (Gmelin, 1791) from the Colombian Caribbean. Penchaszadeh (1984) studied some aspects of the intracapsular development of *Crucibulum marense* Weisbord, 1962, from Venezuela. Hoagland (1986) gave information on some reproductive aspects of *Crucibulum personatum* Keen, 1958, *Crucibulum scutellatum*, *Crucibulum spinosum*, and *Crucibulum umbrella* Deshayes, 1830, from the Pacific coast of Central America.

Most *Crucibulum* species mentioned above have planktonic development and hatch as veliger larvae (*C. personatum*, *C. scutellatum*, *C. spinosum* and *C. umbrella* reviewed by Hoagland, 1986) or veliconch (*C. auricula*, according to Bandel, 1975). Up to now, the only species known to have non-planktonic direct development is *C. marense* (Penchaszadeh, 1984). Neither nurse eggs nor cannibalism among embryos have been reported in any of the *Crucibulum* species.

Herein we describe the egg capsules, intracapsular development of the embryos, and hatching mode of *C. auricula* from Isla Caribe, located on the northeastern coast of Venezuela. The relationship between female size and the number and size of egg capsules, size of the eggs and size of hatchlings was also determined.

MATERIALS AND METHODS

Specimens

Brooding specimens were collected in March 1994 and February 1995 at Isla Caribe, Chacopata, northern Araya Peninsula, Estado Sucre, Venezuela (10°12'11"N, 63°52'57"W) between 0.5 and 1 m depth. There, individuals of *Crucibulum auricula* were found attached to large flat rocks set in a patchy habitat of sand and turtle grass (*Thalassia testudinum*). They were easily identified by the edge of the inner cup, which is entirely free (figure 1) and the outer shell, which is beige with coarse ribbons (descriptions in Abbott, 1974, Díaz and Puyana, 1994). Some of the individuals were fixed in a glucamine-acetate (GA) buffer containing 1.6 % formalin (Miloslavich and Penchaszadeh, 1997) and others were kept alive in tanks at 25–27° C and 35 ‰ salinity with aerated, non-circulating seawater.

Voucher adult material of *C. auricula* (entire individuals fixed in formalin and preserved in ethanol) has been deposited in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, catalogue number MCZ 304128.

Table 1. *Crucibulum auricula*. Characteristics of embryos during intracapsular development. Values represent mean ± SD, numbers in parentheses indicate range.

Stage	Characteristics	Size (µm)
1 Egg	Uncleaved yellow egg.	218.1 ± 16.0 (195–236) n = 99
2 Embryo	Developing embryos begin to ingest nurse eggs.	362.4 ± 82.4 (236–472) n = 99
3 Embryo	Nurse egg ingestion ends. Cannibalism among sibling embryos begins.	615.7 ± 82.9 (472–786) n = 105
4 Early veliger	Cannibalism ends. Early veliger with round velum, small foot, eyes, short and thick cephalic tentacles, organic matrix of shell.	701.0 ± 78.5 (511–786) n = 69
5 Veliger	Veliger with velum measuring 250 µm in diameter, pigmented with white spots, non-calcified protoconch, enlargement of foot.	726.1 ± 61.2 (629–825) n = 64
6 Pediveliger	Prehatchling with reduced velum (less than 200 µm), long and thin cephalic tentacles, long foot with edge pigmented (measures 1 mm), calcification of shell (yellowish) begins. Packed yolk in the posterior region of the animal.	740.5 ± 69.6 (629–825) n = 13
7 Hatching	Crawling juvenile, absence of velum, cilia remain, foot with two lobes in the anterior part, calcified brown shell, little to no yolk reserves.	728.0 ± 70.0 (680–840) n = 10

Development

We studied 30 females of *C. auricula*. In each spawn we observed: (1) the number and size of egg capsules brooded per female, (2) the number and size of eggs and developing embryos within the capsule, (3) the different stages of development, and (4) the hatching mode. The 30 females produced a total of 373 egg capsules; of these we randomly chose 125 egg capsules (between 1 and 10 from each female). Egg capsules were separated from the cluster, classified according to stage of development, and kept in 30 ml beakers inside tanks

with aerated and Millipore-filtered (Whatman GF/B) seawater. Filtered seawater was renewed daily. Egg capsules were incubated in the dark at 26 °C in a Precision (818) incubator.

Observations of live and preserved material was done with a ZEISS dissecting microscope and a ZEISS compound microscope; measurements were taken with an ocular micrometer. Results are reported as mean ± standard deviation.

RESULTS

The shell diameter and height of sexually mature females of *C. auricula* ranged from 12 to 23 mm (18.4 ± 2.6 mm, n = 30) and from 6 and 10 mm (7.6 ± 1.4 mm, n = 16) respectively. A significant correlation was found between female shell diameter and capsule size (Pearson correlation coefficient r = 0.54, $p < 0.01$), that is, larger females brooded larger egg capsules. However, no significant correlation was found between female diameter and the number of capsules, eggs per capsule, number of hatchlings, nor hatchling size.

Development

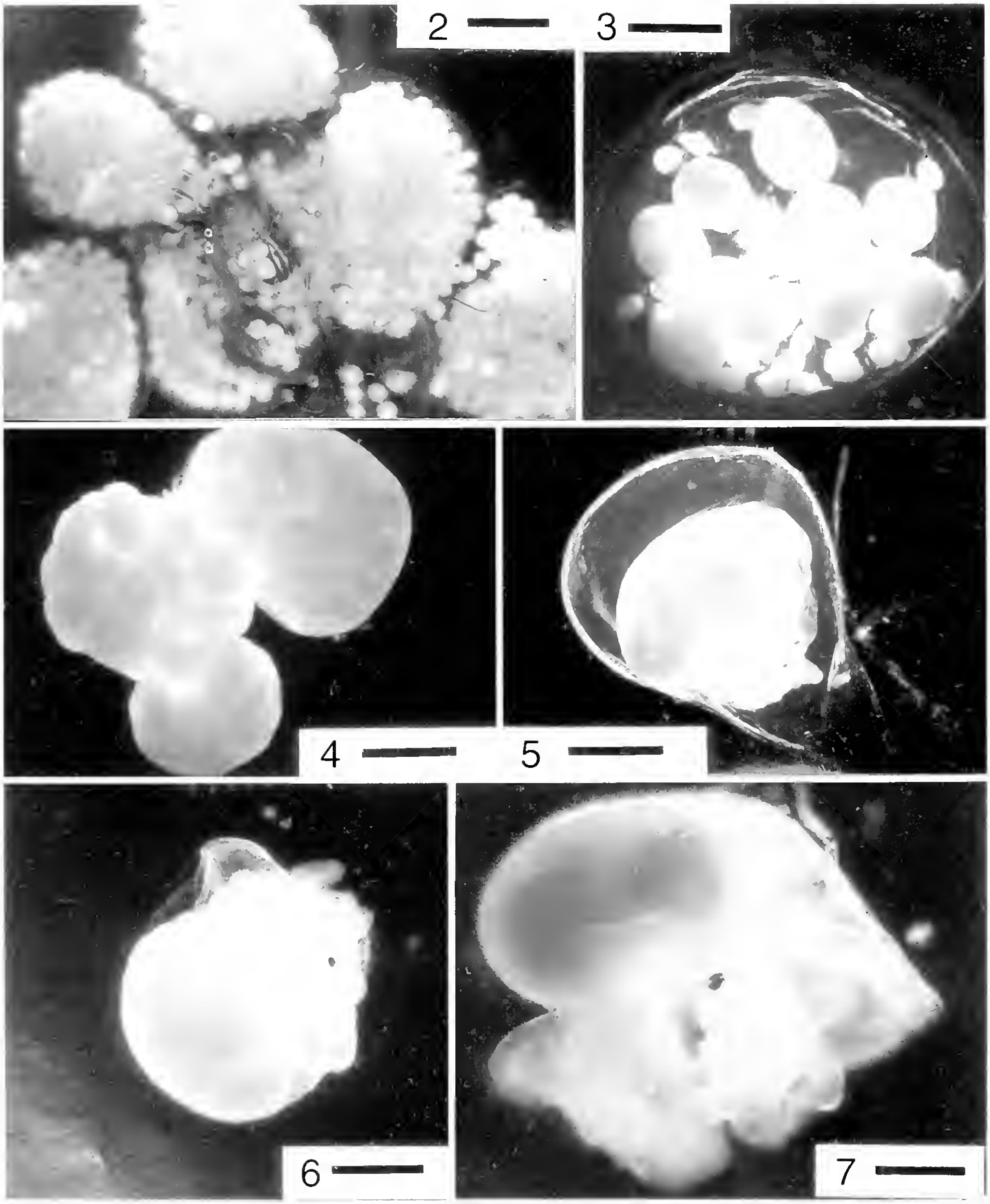
Females brooded between 4 and 20 egg capsules in the mantle cavity (12.4 ± 4.4, n = 30). Egg capsules had a triangular shape, with one corner extending to form a stalk, and were attached to the substrate at the base of this short stalk. The stalks are flattened only at the base of the capsule and the rest is thread-like. The capsule walls were thin, fragile, transparent (figure 2) and the egg capsule was turgid. No exit plug was observed. Egg capsules measured between 1.6 and 3.5 mm lengthwise (without the stalk) (2.5 ± 0.3 mm, n = 125) and 1.0 to 2.8 mm wide (2.1 ± 0.3 mm, n = 125).

The number of eggs per capsule varied from 55 to 305 (161 ± 56, n = 56). Uncleaved eggs were yellow and measured approximately 220 µm in diameter (figure 2). All eggs underwent the first four cleavages. 93% arrested development at this stage and were ingested by the remaining developing embryos (between 3 and 24 per egg capsule, 11.0 ± 6.0, n = 21) as nurse eggs. Within the capsules from a single female, embryos developed synchronously. Gastrulation is accomplished when the ectoderm undergoes epiboly from the animal pole and envelops the other cells of the embryo. Developing embryos measured about 362 µm when they started to ingest the whole nurse eggs, they were oval-shaped, yellow, with no velar lobes nor shell (figure 3). At the end of the ingestion stage, these embryos measured about 616 µm in length; they were yellow and the nurse eggs were tightly packed in their interior. At this point of their development, the embryos started to cannibalize each other. It was common to find two embryos feeding upon a third one (figure 4). After the cannibalism stage, 1 to 11 embryos remained in each capsule (7.0 ± 3.0, n = 21) and developed the velar lobes. The early intracapsular veliger measured about 700 µm and was characterized by a small round velum, a small foot, eyes, very short and thick cephalic tentacles and surrounded by an organic matrix (figure 5). A fragile shell measuring around 726 µm developed from the organic matrix. The developed velum measured 250 µm in diameter and had white spots (figure 6). The intracapsular pediveliger stage had a reduced velum measuring less than 200 µm in diameter, had elongated and thin cephalic tentacles, and a long foot (about 1 mm) with brown lines along the edges. When calcification started (figure 7), the pediveliger shell measured about 740 µm. Pediveligers were not able to swim when excapsulated into seawater. A few days prior to hatching (6 to 7 days), yolk was observed inside of the pediveligers. These yolk reserves disappeared almost completely by hatching, and only a small yellow spot in the posterior region of the animal remained. Hatching occurred as crawling juveniles with a brown calcified shell measuring 730 µm in length, the shell was relatively smooth with thin horizontal lines separated 20 µm from each other; juveniles had a well-developed foot with a small and transparent operculum, short cephalic tentacles and no velum. However, ciliary movement was observed in the region where the velum had been resorbed (table 1).

DISCUSSION

The relationship between female size and some reproductive parameters such as capsule size, number of eggs and developing embryos within each capsule, and hatching size of the juveniles has been reported in several families of marine gastropods (Spight *et al.*, 1974, in Muricidae; Robertson, 1983, in Epitoniidae; Miloslavich and Dufresne, 1994, in Buccinidae). These studies indicate that larger females produce bigger egg capsules that contain more eggs and more and bigger hatchlings than smaller females. In *Crucibulum auricula* we found that larger females brood larger egg capsules than small females; however, these egg capsules do not contain more eggs nor produce more or bigger hatchlings, therefore the reproductive outcome of both small and large females is the same. Chaparro *et al.* (1999) found no relationship between female size and the number of developing embryos of *Crepidula dilatata* Lamarck, 1822, however, the mean size of the juveniles at hatching did increase with the shell length of the female, because more nurse eggs were available to an embryo from a larger female than to an embryo from a smaller one.

In calyptraeids, the number of egg capsules per brood is usually related to female size (see table 3 in Hoagland, 1986). *Crucibulum auricula* is one of the smallest species of *Crucibulum*. The number of egg capsules (mean 12 egg capsules per brood) in this species is one of the lowest among the five species of the genus for which there is information on reproduction published. It is similar to that of *C. marense* (about 14 egg capsules) but it is lower than *C. scutellatum*, *C. spinosum* (both with a mean of 20 capsules), and *C. personatum* (30 capsules). The production of hatchlings of *C. auricula* is also



Figures 2–7. Intracapsular development of *Crucibulum auricula*. **2.** General view of the egg capsules with uncleaved eggs (stage 1). Scale bar = [illegible]. **3.** Egg capsule containing both developing embryos (large) and nurse eggs (small) (stage 2, adelphophagy). Scale bar = [illegible]. **4.** Cannibalism among sibling embryos (stage 3). Scale bar = 200 μm. **5.** Early veliger inside egg capsule (stage 4). Scale bar = 250 μm. **6.** Veliger with non calcified protoconch (stage 5). Scale bar = 250 μm. **7.** Prehatching (stage 6). Scale bar = [illegible].

Table 2. Brood characteristics and total production of hatchlings within the genus *Crucibulum*. NA = not available.

Species	Egg size (µm)	No. capsules	No. hatchling/capsule	Total hatchling production	Hatchling size (µm) mode	Source
C. marense	NA	14	14.5	203	1020–1060 Crawler	Penchaszadeh, 1984
C. personatum	NA	30	275	8250	320 Veliger	Hoagland, 1986
C. scutellatum	NA	20	200	4000	NA Veliger	Hoagland, 1986
C. spinosum	NA	20	200	4000	280 Veliger	Hoagland, 1986
C. umbrella	NA	31	150	4650	440 Veliger	Hoagland, 1986
C. auricula	218	12	7	84	728 Crawler	This work

very low (about 84 crawling juveniles), followed by *C. marense* with a total production of 200 crawling juveniles. The other *Crucibulum* species produce veliger larvae in numbers over 4000 (Hoagland, 1986) (table 2).

The size of the uncleaved egg is very important because it determines the amount of yolk available for the embryo to develop when other extraembryonic food sources such as nurse eggs, cannibalism among siblings, or intracapsular fluid, are not available. The egg of *Crucibulum auricula* is within the size range of calyptraeid species in the genus *Crepidula*, which vary between 150 and 420 µm (Hoagland, 1986). Within the genus *Crucibulum*, the egg size has been previously reported only for *C. spinosum* (from 170 to 190 µm; Coe, 1938).

Within calyptraeids and particularly in the genus *Crepidula*, two feeding modes during intracapsular development have been described: adelphophagy, or nurse egg ingestion, and cannibalism; both were observed in *C. auricula*. Hoagland (1986) reviewed the patterns of encapsulation and brooding in calyptreids and reported no nurse eggs in the five *Crucibulum* species for which we have data (*C. personatum*, *C. scutellatum*, *C. spinosum*, *C. umbrella*, and *C. marense*). However, Coe (1938) reported that a considerable proportion of the eggs of *C. spinosum* fail to complete development, as the number of veliger larvae that hatch is much lower than the original number of eggs. This difference between number of eggs and number of hatching veligers could be due not only to nurse eggs but also to embryos ingested. Thorson (1940) reported that the large size of the embryos at hatching (0.7 mm) in *C. scutellatum* from the Persian Gulf was probably due to cannibalism and that nurse eggs do not seem to occur. If properly identified by Thorson, this species would have a very wide geographic range even for a species with planktonic development (Hoagland, 1986), since Keen (1971) and Abbott and Dance (1982) reported it as a tropical western American species ranging from Mexico to Ecuador. Penchaszadeh (1984) stated, for *C. marense*, that presumably neither nurse eggs nor cannibalism are involved during development given the uniformity of shell size at hatching and because undeveloped eggs were not observed.

Bandel (1975; 1976) reported that *C. auricula* from the Colombian Caribbean produces 10 to 12 yellowish eggs and that all develop into a veliconch possessing a functional foot and a large velum. His observations were probably carried out after the developing embryos finished eating the nurse eggs, which could have led him to misinterpret the embryos as eggs and to not observe the 150 nurse eggs per capsule we observed (93 % nurse eggs). Another possibility is that he worked with a different species. In the Colombian Caribbean, Díaz and Puyana (1994) have reported three *Crucibulum* species, *C. auricula*, *C. marense* and *C. planum*; the first two are relatively common and the third one is uncommon. The shell of *C. marense* is similar in size to *C. auricula* (15 mm in diameter) but is characterized by a curved apex; the shell of *C. planum* is much larger (40 mm in diameter) and is characterized by brown reddish spots. Given that the taxonomy of all calyptraeids, especially *Calyptraea* Lamarck, 1799, and *Crucibulum* is on need of major revision, Bandel probably misidentified the species. However, if Bandel's observations are correct and he properly identified the species, this would be a unique case of poecilogony among gastropods, which, we suggest, is unlikely to happen (see reviews by Bouchet, 1989, and Hoagland and Robertson, 1988).

Embryos of *C. auricula* develop synchronously within the capsules of a single female. However, they reach variable sizes (between 680 and 840 µm) probably depending on the number of nurse eggs and embryos ingested. Hoagland (1986) reported that, for most Calyptraeidae, larvae develop synchronously, except in those species with nurse eggs, and in *Crucibulum spinosum* there is asynchrony between egg capsules, implying that the brood does not hatch all at once.

Most *Crucibulum* species herein mentioned (*C. personatum*, *C. scutellatum*, *C. spinosum*, *C. umbrella*) hatch as free-swimming veligers (Hoagland, 1986; Coe, 1949). Penchaszadeh (1984) reported crawling juveniles for *C. marense* and Bandel (1975; 1976) reported veli-

conchs for *C. auricula* in the Colombian Caribbean. In this study, we found that *C. auricula* hatches as crawling juveniles, with some velar (ciliar) remains but are unable to swim. Even in the absence of a free-swimming stage, this species has a wide geographic distribution in the western Atlantic, from the coast of South Carolina south to the Caribbean to tropical Brazil (Abbott, 1974; Díaz and Puyana, 1994).

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The family Mitridae (Gastropoda) in the Lower Miocene Chipola Formation of northern Florida

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ABSTRACT

A brief review of the Mitridae from the Lower Miocene Chipola Formation of northern Florida is presented, with the description of two new species and the identification of adult specimens of *Mitra acteoglypha* Gardner, 1937. The new species are *Mitra calhounensis*, a common, large fusiform species that bears a resemblance to *Mitra fusiformis* (Brocchi, 1814) from the Miocene of Europe, and *Scabricola chipolana*, a rare, smooth-shell, species that is limited to the ancient reef environment along Tenmile Creek and the Chipola River.

Additional key words: Neogene, *Mitra*, *Scabricola*, *Ziba*

INTRODUCTION

According to Cernohorsky (1976), the family Mitridae is characterized by "fusiform, elongate-ovate or cylindrical shells which have convex or angulate whorls, usually a narrow aperture, from 3 to 11 folds on the columella and a distinct siphonal notch." Members of this family are found in tropical to temperate waters throughout the world where they thrive in intertidal areas down to depths not exceeding 1465 m (Cernohorsky, 1976). The first fossil evidence of this family appeared in Upper Cretaceous deposits and numerous other fossil species have been collected and described from Tertiary deposits throughout the world (Cernohorsky, 1976).

Gardner (1937) reported 16 species of Mitridae from the Alum Bluff Group of Florida, "with probably as many more represented by material too imperfect to describe." Of the 16 Alum Bluff species, Gardner listed 11 from the Chipola Formation. Of these, eight are now classified in Costellariidae and one, *Mitra* (*Pleioptygma*) *prodroma* Gardner, 1937, has been placed in the Pleioptygmatidae (Quinn, 1989). Currently, only *Ziba illacidata* (Woodring, 1928) (= *Mitra mitrodita* Gardner, 1937) and *Mitra acteoglypha* Gardner, 1937 remain in the Mitridae.

The objectives of this paper are to: (1) describe two new species of Mitridae from the Chipola Formation of northern Florida and, (2) update the taxonomic status of the two remaining species from the Chipola Formation.

Type and figured specimens referred to in this paper are deposited in the paleontological collections at the United States National Museum, Smithsonian Institution (USNM) and the Florida Museum of Natural History, University of Florida (UF).

SYSTEMATICS

Family Mitridae Swainson, 1831
Genus *Mitra* Lamarck, 1798
Subgenus *Mitra* Lamarck, 1798,
Mitra (*Mitra*) *acteoglypha* Gardner, 1937
(Figures 1–3)

Description: Shell fusiform-ovate, moderately heavy. Protoconch usually eroded. Sutures deeply impressed. Spire with 5 convex whorls sculptured with punctated, evenly spaced spiral grooves. Last whorl with 20–28 spiral grooves, penultimate whorl with 7–10, and remaining whorls with 6–7. Aperture narrow, more than half shell length. Outer lip thin, not lirate within. Parietal wall very thin. Columellar folds 4–5, sharply elevated, oblique, equally spaced, increasing in prominence in posterior direction. Anterior canal moderately long, not sharply defined, broadly emarginate at the extremity; anterior fasciole slightly swollen.

Material examined: UF 95999, length 41.3 mm, width 15.1 mm; UF 96000, length 43.9 mm, width 15.1 mm.

Type locality: USNM locality 2213, 1 mile below Bailey's Ferry, Chipola River, Calhoun County, Florida.

Distribution: *Mitra acteoglypha* is a moderately rare species that has been found at two Chipola Formation sites along Tenmile Creek in Calhoun County, Florida, and at a single site along Farley Creek in Calhoun County. According to Vokes (1989), the sites along Tenmile Creek probably represent an ancient reef environment while those at Farley Creek suggest a back-reef habitat.

Discussion: Gardner (1937) described *M. acteoglypha* from a single, broken, juvenile specimen (figure 1). Since the juvenile specimens of all three species of mitrids examined for this paper had spiral grooves similar to *M. acteoglypha* it became necessary to obtain the type specimen and compare it to material from the Florida Museum of Natural History and the investigator's

collection in order to determine which of the adults bore the greatest similarity to the juvenile described by Gardner (1937). After careful comparison of the type with recently collected adult and juvenile specimens, it was apparent that the mitrid illustrated in figures 2–3 was the adult form of *M. acteoglypha*. This decision was based upon the fact that both had similar shell shapes, the whorls of both bear the punctated spiral sculpturing described by Gardner (*op. cit.*), and both had a similar number of columellar folds. The specimen illustrated in figures 2 is most similar to the holotype. Like the holotype, it has 5 columellar folds and nearly the same number of punctated spiral grooves on the last whorl (26 versus 28 in the holotype). The specimen in figure 3 has only four columellar folds and about 20 punctated spiral grooves on the last whorl. Further examination of 3 partially broken adult specimens in this investigators collection revealed that all had 4 columellar folds.

Among New World fossil mitrids only the Miocene *Mitra almagrensis coralliophila* Olsson, 1922, from northern Peru, bears some resemblance to *M. acteoglypha*. Olsson (1922) described *M. coralliophila* as a shell sculptured with slightly elevated spiral cords separated by finely sculptured grooves. In *M. coralliophila* there is a total of five spiral cords on each of the whorls except for the last, and the columella bears 3 prominent folds. *Mitra acteoglypha* differs from *M. coralliophila* by its larger size (41.3 mm and 43.9 mm for the adults versus 17 mm), larger number of spiral cords (10 versus 5), and its larger number of columellar folds (4–5 vs. 3).

Because of strong similarities between these two species, Cernohorsky (1976) believed that *M. acteoglypha* might be related to the recent *Mitra barbadensis* (Gmelin, 1791). However, *M. barbadensis* entirely lacks the punctated spiral grooves that characterize *M. acteoglypha*. Among extant species, *M. acteoglypha* seems to bear a stronger resemblance to the Indo-Pacific *Mitra ambigua* Swainson, 1829. A comparison of these two species shows similar shell morphologies, with shells of the two species showing punctated spiral grooves. However, *M. acteoglypha* is a smaller species (43.9 mm length vs. 53.4 mm) with fewer columellar folds (4–5 vs. 5–6) and a fewer number of punctated spiral grooves (20–28 vs. 25–35).

Subgenus *Fusimitra* Conrad, 1855
Mitra (Fusimitra) calhounensis new species
(Figures 4–5)

Description: Shell slender, large, moderately heavy, fusiform ovate. Protoconch usually eroded. Suture deeply impressed. Spire with 8–9 weakly convex whorls. First six teleconch whorls sculptured with 7–8, evenly spaced, pitted spiral grooves. Pitted spiral sculpturing on remaining teleconch whorls faint, disappearing near the aperture. Aperture slightly shorter than spire, narrow and elongate, smooth within. Columella with thin callus in adult specimens and 5–6 strong, oblique, equally spaced folds. Siphonal fasciole straight, siphonal notch distinct.

Holotype: UF 95998, length 92.1 mm, width 24.3 mm.

Paratypes: Paratype A, UF 87784, incomplete specimen, length 60.5 mm, width 18.3 mm, Chipola Formation, north bank of Tenmile Creek at powerline crossing about one mile west-northwest of mouth of creek at "Bailey's Ferry" (SE 1/4 Sec. 12, T1N, R10W), Calhoun County, Florida (Tulane University locality TU 830). Paratype B, UF 89579, incomplete specimen, length 62.0 mm, width 20.8 mm. From type locality.

Type locality: Chipola Formation, Tenmile Creek, about 1.75 miles west of Chipola River (NE 1/4 Sec. 12, T1N, R10W), Calhoun County, Florida (Tulane University locality TU 546; = USGS 2212, "one mile west of Bailey's Ferry").

Distribution: Only one complete specimen of *M. calhounensis* is known. However, numerous fragments of this shell are present in the Tulane University Collection, now housed at the Florida Museum of Natural History, Gainesville. In addition, the investigator has obtained numerous shell fragments over the last ten years from a broad range of Chipola Formation collecting sites along Tenmile and Farley creeks and both banks of the Chipola River.

Etymology: Named after Calhoun County, Florida.

Discussion: From the examination of numerous shell fragments it is evident that *M. calhounensis* attained a very large size with many specimens reaching total lengths in excess of 110 mm. In general shell shape and size of this species bears a strong resemblance to the living Mediterranean *Mitra fusiformis zonata* Marryat, 1818, and its fossil counterpart *Mitra fusiformis fusiformis* (Brocchi, 1814) from the Miocene and Pliocene deposits of Portugal, France, Italy, Austria, Hungary, Poland, England, and the Island of Rhodes. It is very likely that *M. fusiformis* and *M. zonata* share a common ancestor with *M. calhounensis*.

Mitra fusiformis can be distinguished from *M. calhounensis* by the more slender shell and presence of well-developed pitted spiral grooves on the first five teleoconch whorls of the latter species. Among New World Neogene species, *M. calhounensis* bears some resemblance to *Mitra titan* (Gabb, 1873) from the Pliocene deposits of the Dominican Republic as well as the Late-Pliocene species, *Mitra woodringi* Olsson, 1964, from the Esmeraldas Formation of Equador, and *Mitra swainsonii dunbari* Olsson, 1932, from the Pliocene Tumbez Formation of northern Peru. Both *M. titan* and *M. calhounensis* are fusiform-elongate shells reaching lengths in excess of 110 mm with the early teleconch whorls having distinct spiral sculpturing. However, *M. calhounensis* has a thinner lip and has 5–6 columellar folds. In addition, the spiral sculpture on the early whorls of *M. titan* has fine spiral grooves with every

fourth one deeper (Pilsbry, 1922), while in *M. calhounensis* the spiral grooves are all the same depth on the early whorls.

Mitra swainsonii dunbari and *M. woodringi* are very similar and may represent the same species. This similarity was noted by Cernohorsky (1976), who considered *M. woodringi* to be conspecific with *M. swainsoni dunbari*. Abbott (1974) also listed *M. woodringi* as a synonym of *Mitra swainsonii swainsonii* (Broderip, 1836), an uncommon Recent "subspecies" that lives in deep water from South Carolina to the West Indies. *Mitra calhounensis* is similar to *M. woodringi* and *M. swainsoni dunbari* in that it is a fusiform-elongate shell with distinct spiral sculpturing on the early whorls. However, unlike the latter, *M. calhounensis* has a less stout and twisted anterior canal, it has 5–6 columellar folds, and has fewer spiral grooves on the apical whorls.

Among extant taxa, *M. calhounensis* is also similar to *Mitra swainsonii antillensis* Dall, 1889. Cernohorsky (1976) listed this as a deep-water subspecies that occurs from North Carolina to Yucatan and the Antilles. Like *M. calhounensis*, *M. swainsonii antillensis* has 5–6 columellar folds and has well-developed spiral sculpture. However, *M. calhounensis* has a more slender shell shape, more deeply impressed sutures, fewer spiral grooves, and the spiral sculpturing disappears near the aperture. It is possible that *M. calhounensis* is the fossil ancestor to the present day *M. swainsonii* complex from the Caribbean province.

New World ancestors to the fusiform-shaped *M. calhounensis* date back to the Cretaceous. These include *Paleofusimitra elongata* Sohl, 1963, from the Cretaceous Ripley Formation of Mississippi (Sohl, 1964); *Fusimitra millingtoni* (Conrad in Wailes, 1854) from the Eocene Moody's Branch Formation in Mississippi (Dockery, 1977) and *Mitra conquisita* Conrad, 1885 from the Lower Oligocene of the Vicksburg Group in Mississippi (MacNeil and Dockery, 1984).

Subfamily Imbricariinae Troschel, 1867
Genus *Ziba* H. and A. Adams, 1853
Ziba illacidata (Woodring, 1928)
(Figures 6–7)

Mitra (Tiara) henekeni illacidata Woodring, 1928, pp. 243, pl. 14, fig. 13 ("Miocene" [Late Pliocene] Bowden Formation, Jamaica);

Mitra (Tiara) mitrodita Gardner, 1937, pp. 408–409, pl. 48, figs. 10–11 ("1 mile below Bailey's Ferry, Chipola River, Calhoun County, Fla.").

Description: Shell fusiform, moderately slender. Protoconch glossy, with 3 whorls. Sutures deeply impressed. Teleconch whorls 7, convex, sculptured with strong spiral cords and axial threads. Four spiral cords on the spire whorls. Aperture narrowly lobate, about half shell length. Outer lip thin, the margin crenate in harmony with the external sculpture. Parietal wall thinly glazed. Columellar folds 3, oblique, equally spaced, posterior fold more highly elevated. Siphonal notch narrow, deep.

Holotype: USNM 369433, length 10 mm, width 6.7 mm.

Type locality: Late Pliocene Bowden Formation, Jamaica.

Distribution: Bowden Formation in Jamaica and Chipola Formation sites along Tenmile Creek, Farley Creek, and the Chipola River in northern Florida.

Remarks: *Ziba illacidata* belongs to a group of moderately small mitrids that are sculptured with a presutural carina, spiral grooves or cords and axial lirae in the interspaces. Cernohorsky (1991) tentatively placed mitrids with these characteristics in the separate genus *Ziba* until the radula of living species could be examined and compared with those belonging to the genus *Cancilla*.

Ziba illacidata was described by Woodring (1928) from the Late-Pliocene Bowden Formation of Jamaica. Later Gardner (1937) found a similar species in the early Miocene Chipola Formation deposits of northern Florida and named it *Mitra mitrodita*. Cernohorsky (1991), after examining both *Mitra illacidata* and *Mitra mitrodita* stated that both shells are identical and, irrespective of the age difference, listed *M. mitrodita* in the synonymy of the geologically younger *M. illacidata*. This arrangement is followed herein and, for comparison purposes, the holotypes of *M. illacidata* and *M. mitrodita* are illustrated in figures 6–7.

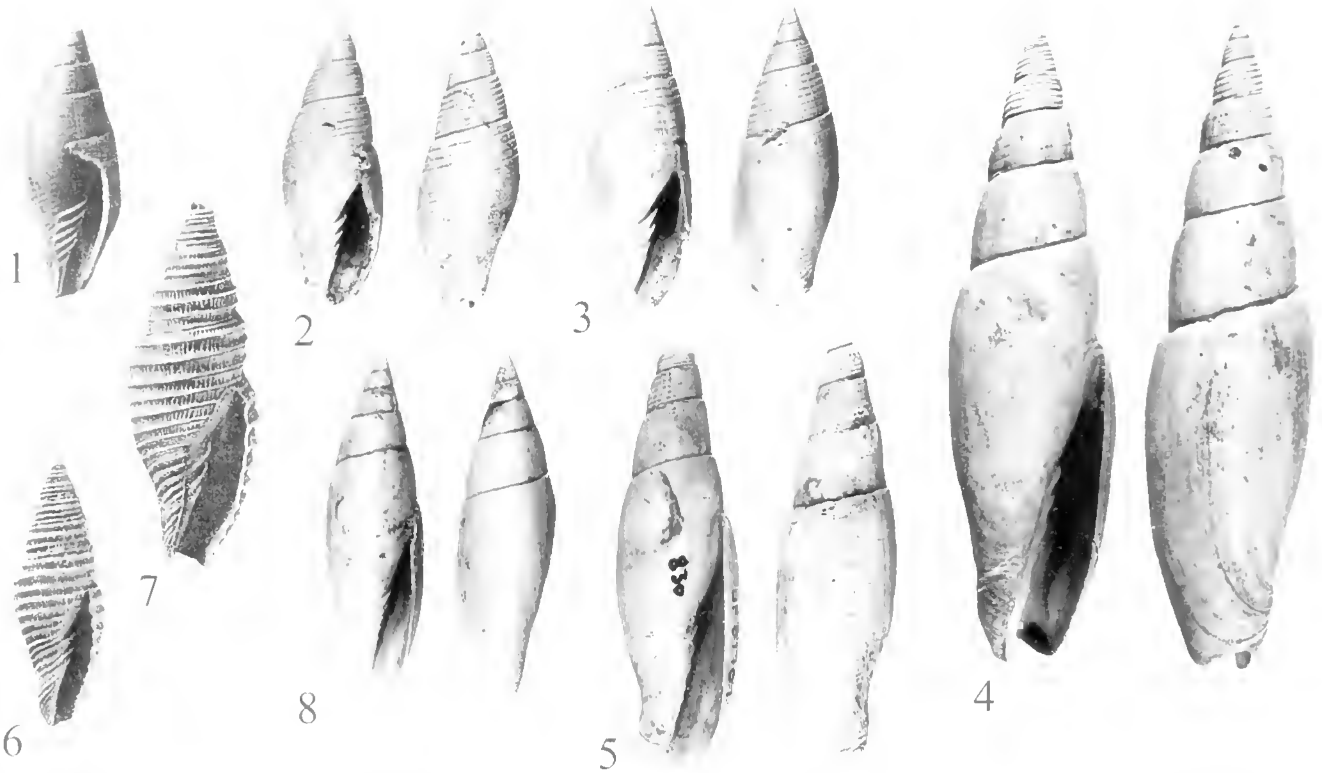
Genus *Scabricola* Swainson, 1840
Subgenus *Swainsonia* H. and A. Adams, 1853
Scabricola (Swainsonia) chipolana new species
(Figure 8)

Description: Shell fusiform-elongate, moderately solid. Protoconch eroded. Suture distinct, impressed. Teleconch whorls 7, weakly convex, sculptured with 7–8 pitted spiral grooves on the early whorls. Spiral grooves very faint or absent on the penultimate and last whorl. Aperture half the length of the spire, elongate, fairly narrow and smooth within. Outer lip thin, outer edge smooth. Columella with thin callus, callus more prominent anteriorly. Columellar folds 4–5, moderately strong, oblique, equally spaced and of equal size. Siphonal fasciole straight or slightly recurved, siphonal notch prominent.

Holotype: UF 95997, length 50.2 mm, width 14.7 mm.

Type locality: Chipola Formation, Tenmile Creek, about 1.25 miles west of Chipola River (SE 1/4 Sec. 12, T1N, R10W), Calhoun County, Florida (Tulane University locality TU 951).

Distribution: *Scabricola chipolana* is a very rare species that has only been collected from two localities along Tenmile Creek and a single location along the Chipola River. The two sites along Tenmile Creek are sep-



Figures 1–8. Mitridae from the Lower Miocene Chipola Formation, Florida. **1–3.** *Mitra (Mitra) acteoglypha* Gardner, 1937. Holotype USNM 114328, length 19 mm, width 7.0 mm (Photograph of illustration in Gardner, 1937; pl. XLVIII, fig. 5). **2.** Selected specimen, UF 95999; length 41.3 mm, width 15.1 mm. **3.** Selected specimen, UF 96000, length 43.9 mm, width 15.1 mm. **4–5.** *Mitra (Fusimitra) calhounensis* new species. **4.** Holotype, UF 95988, length 92.1 mm, width 24.3 mm. **5.** Paratype A, UF 87784, length 60.5 mm (incomplete specimen), width 18.3 mm. **6–7.** *Ziba illaculata* (Woodring, 1928). **6.** Holotype, USNM 369433, length 10 mm, width 6.7 mm (illustration from Woodring (1928) pl. 14, fig. 13). **7.** USNM 371435, holotype of *Mitra mitrodita* Gardner, 1937, length 27 mm, width 8.8 mm (illustration from Gardner, 1937; pl. 48, fig. 10). **8.** *Scabricola (Swainsonia) chipolana* new species. Holotype, UF 95997, length 50.2 mm, width 14.7 mm.

arated by approximately a half mile, and located on opposite sides of the creek.

Etymology: Named for the Chipola River in northern Florida.

Discussion: *Scabricola chipolana* is only known from one complete and two badly broken specimens. It is less bulbous and lacks the pronounced spiral sculpture characteristic of *Mitra acteoglypha* Gardner (1937), and is much smaller and more slender than *Mitra calhounensis*. The distinctive shell shape of *S. chipolana* rendered generic allocation difficult. An initial review of fossil and extant New World mitrids by this investigator revealed that *S. chipolana* was not compatible with any known species. However, a comparison of this shell with Indo-Pacific species showed that its shell features were most similar to those in the genus *Scabricola*. Members of this genus reach a length of [illegible] mm, have 5–8 convex or subangulate whorls, are sculptured with deep, punctated, or striated grooves, have an aperture that is equal in length or longer than the spire, a columella with 6–8 oblique folds, and have a distinct siphonal notch. *Scabricola chipolana* was assigned to the subgenus *Swainsonia* because of its slender and smoother appearance and the punctated spiral sculpture was confined to the early spire whorls. Among extant Indo-Pacific species *S. scabricola* bears some resemblance to the shallow-water, sand-dwelling subspecies *Scabricola (Swainsonia) casta* (Gmelin, 1791). However, *S. casta* has a stouter shell shape, fewer punctated spiral grooves on the early spire whorls (3 vs. 7), fewer columellar folds (4–5 vs. 5–6), and its columellar folds are situated more toward the anterior end. *Scabricola chipolana* is the first and only known example of this genus from the New World. Only one fossil example of this genus, *Scabricola (Scabricola) desetangsii* (Kiener, 1838), has been reported from the Pliocene of the Indo-Pacific (Cernohorsky, 1991), and there are no known fossil representatives of the subgenus *Swainsonia*.

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Pisidium chiquitanum new species from Santa Cruz de la Sierra, Bolivia (Bivalvia: Sphaeriidae)

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ABSTRACT

A new species of *Pisidium* C. Pfeiffer, 1821, from Santa Cruz de La Sierra, Bolivia, is here described. *Pisidium chiquitanum* new species is defined by the striking ovate shell outline, backward displaced beaks, enclosed ligament pit, and by the presence of two siphonal apertures and two demibranchs on each side.

Additional key words: South America, freshwater, bivalve, clam.

INTRODUCTION

Little is known about the species of the genus *Pisidium* C. Pfeiffer, 1821, in Bolivia. At present, only two species have been reported from that country: *Pisidium meierbrooki* Kuiper and Hinz, 1984, described from a pond at 1100 m altitude at Cordillera de los Frailes (19°34′ S, 65°45′ W, eastern Potosí, Bolivia), also reported from Nubi Lake (15° S, 69° W) at 4600 m altitude, near Ulla Ulla, and *Pisidium vile* Pilsbry, 1897, recently reported from Estación Parapetí, Santa Cruz de la Sierra (Ituarte, 1995).

The species originally described as *Pisidium (Pisidium) titicacense* Pilsbry, 1924, and *Pisidium boliviense* Sturany, 1900) actually belong to the genus *Sphaerium* Scopoli, 1777 (Kuiper and Hinz, 1984). Additionally, *Cyclas forbesi* (Philippi, 1869) was erroneously cited by Pilsbry (1911) as a *Pisidium* species. *Pisidium chiquitanum* new species from Santa Cruz de la Sierra, Bolivia, is described in the present work.

MATERIALS AND METHODS

The source of material is described in the systematics section. The specimens were fixed immediately after collection in 80% ethanol. Specimens for scanning electron microscopy were cleaned by repeated rinsing in distilled water followed by a short treatment (2–3 seconds) in a 10% sodium hypochlorite solution. For periostracum removal several specimens were treated with a concentrated solution of commercial sodium. Linear measurements (shell length (SL), shell height (SH), shell width (SW) and pre-siphonal suture (PSS)), morphometric indices and ratios ((height index (HI = SH/SL), convexity index (Ci = SW/SH), ratio hinge length (HiL):shell length (HiL/SL)), were calculated according to the criteria followed by Ituarte (1996). For each calculation (n = 21), mean and standard deviation values are given. For comparative purposes, specimens of *Pisidium magellanicum* (Dall, 1908) from the Princeton University Expedition to Patagonia lodged at the Academy of Natural Sciences of Philadelphia (ANSP) were used.

SYSTEMATICS

Pisidium chiquitanum new species
Figures 1–11

Diagnosis: Distinguishable by somewhat low and markedly oval shell shape, with low and backward located beaks, position of ligament, internal but externally visible, the presence of branchial and anal openings, two demibranchs on each side and nephridia of closed type.

Description: *Shell:* Thin, translucent, of small to medium size (mean SL = 3.9 ± 0.25, maximum observed size: 4.2 mm), not high (mean HI = 80 ± 1), moderately convex (mean Ci = 61 ± 1), shell outline markedly oval, elongate, anterior end produced in a sharp curve, posterior end short, widely rounded, sometimes slightly truncated and straight (figures 2, 3). Beaks low, slightly projected above dorsal margin, narrow, displaced backward, located at about 62% of SL. Shell surface finely and somewhat irregularly striated, dull glossy, straw-yellowish.

Hinge plate solid, hinge line rather long (HiL/SL = 56 ± 2). Hinge: Right valve (figures 4, 5, 8): cardinal tooth (C3) strongly curved in the middle, quite narrow in anterior half, greatly enlarged in a weakly grooved, rounded cup. Lateral teeth robust, inner anterior lateral (AI) long, widely curved, cusp little displaced forward; outer anterior lateral tooth (AIII) quite short, cusp dis-

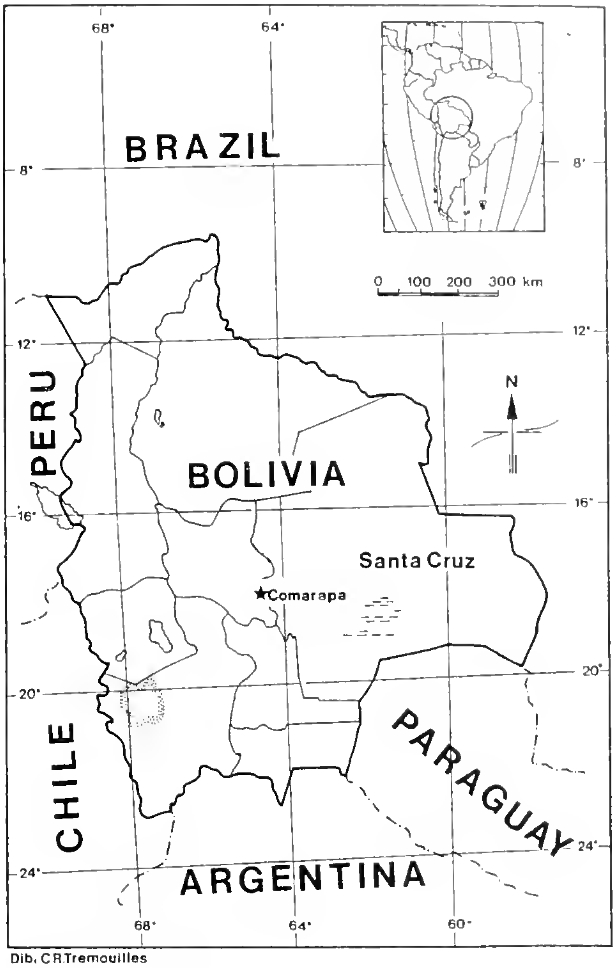


Figure 1. Location map. ★: Type locality.

tal; inner posterior lateral (PI) nearly straight, rather short, cusp sub-central; outer posterior lateral (PIII) reduced in size with distal cusp. Left valve (figures 6, 7): cardinal teeth short, the inner (C_2) triangular, bent upward, slightly oblique in relation to antero-posterior axis, the outer (C_4) a narrow, uniformly curved blade, quite oblique, overlapping C_2 at posterior half; anterior lateral tooth (AII) strong, straight, cusp sub-central; posterior lateral tooth (PII) relatively short and weak, cusp distal. Ligament pit enclosed, deep, inner margin straight to slightly sinuous, concave at posterior end (figure 8). Escutcheon long, lanceolate, well marked by a delicate line (figure 9). Ligament long, strong, internal, even though visible, from outside, in anterior half through a very narrow, and in some cases rather long, gap between valves, never protruded (figures 9, 10). Ligament length is 23 ± 1% of shell length.

Anatomy: Anal siphon and branchial inhalant opening present. Pre-siphonal suture rather long, representing 11 ± 2 % of SL (figure 13). The branchial inhalant opening is determined by a weak fusion of the inner mantle lobes, without muscular sphincter; a weak ventral retractor muscle is present. Anal siphon well-developed, a pair of powerful siphonal retractors present (figure 13). Muscle scars (S scars), corresponding to the inner radial mantle muscles, well marked, lying apart from the pallial line, those corresponding to anal siphon retractors coalescent with posterior adductor muscle scars (figure 11).

Inner and outer demibranchs present. Outer demibranch smaller, formed by 11–15 very short descending filaments, reaching back to the 14–16[th] filament of inner demibranch (figure 12). Brood pouches develop somewhat upward and posteriorly of inner demibranchs (however in contact with, or slightly covered by, the ascending lamella, which is well developed) (figure 14). Each brood pouch contains 3–4 embryos (embryonic shell length: 1.25–1.40 mm). Nephridia of closed type, dorsal lobe variable in shape, commonly subquadrate (figure 12), lateral loop not visible in dorsal view.

Type locality: Unnamed pond at "La Siberia", a site west of Comarapa, Manuel Caballero Province, Santa Cruz de la Sierra Department, Bolivia (figure 1); M. G. Cuezzo coll.; 09/08/1997.

Etymology: The name refers to Chiquitos, aboriginal inhabitants of the lands presently known as "Llanos de Chiquitos" (central-eastern Bolivian plains), near the type locality.

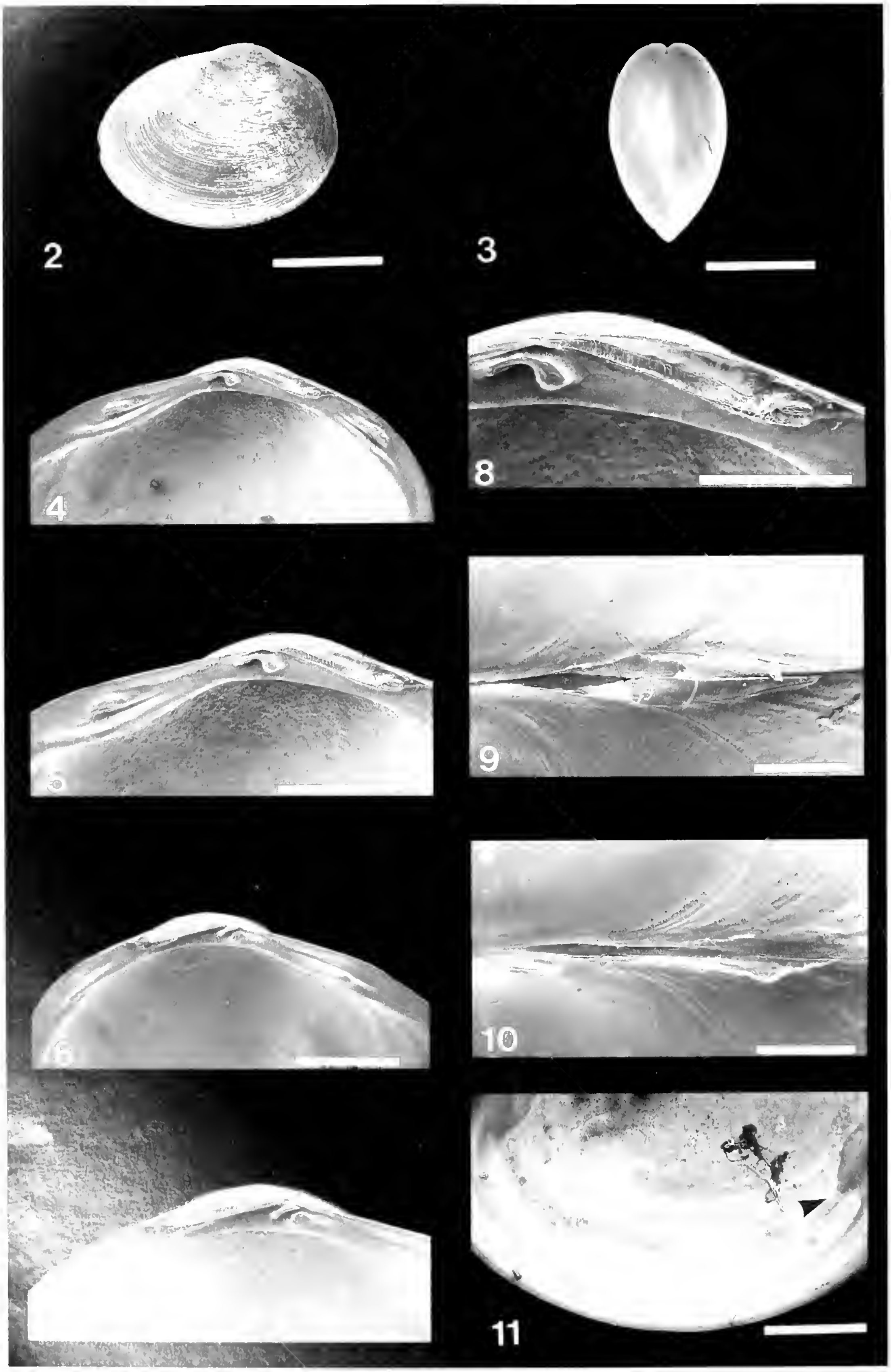
Type material: Holotype and paratypes in the malacological collection, Museo de Historia Natural "Noel Kempff Mercado", Santa Cruz de la Sierra, Bolivia (MHNB 34734). Other paratypes: Department of Invertebrates, Museo de La Plata (MLP 5362); Department of Invertebrates, Museo Argentino de Ciencias Naturales (MACN 34734); Fundación Instituto Miguel Lillo, Tucumán, Argentina (FIML 14235 and 14236); and Muséum national d'Histoire Naturelle, Paris (MNHN unnumbered).

DISCUSSION

Pisidium chiquitanum new species can be easily identified among South American *Pisidium* species by its striking oval shell outline with low and narrow beaks and internal (however visible from exterior) ligament. The new species is also characterized by two, inner and outer demibranchs on each side, two siphonal openings and nephridia of closed type.

Pisidium chiquitanum new species resembles *Pisidium meierbrooki* Kuiper and Hinz, 1984 from Peru and Bolivia, which is the only known species from tropical South America with both, branchial and anal siphonal openings (Ituarte, 1995). *P. meierbrooki* differs from *P. chiquitanum* in having a more convex shell (Ci = 77–80), fuller and more backward displaced beaks.

Pisidium chiquitanum new species is most similar to those specimens from Ecuador and Peru figured and reported by Kuiper and Hinz (1984) as *Pisidium casertanum* (Poli, 1791), a Eurasian species, extremely variable in shell shape and currently regarded as cosmopol-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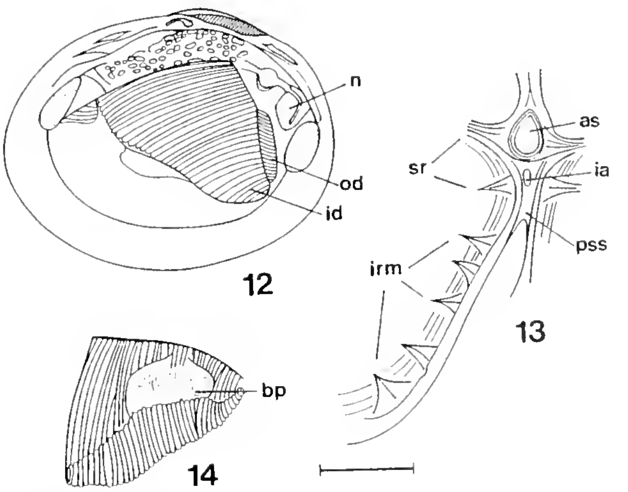
Figures 2–11. *Pisidium chiquitanum* new species. **2.** Holotype (MHNB). **3–11.** Paratypes MLP 5362. **3.** Posterior view of a specimen. **4.** Hinge of a right valve. **5.** Right valve, detail of cardinal tooth, ligament and anterior lateral teeth. **6.** Hinge of a left valve. **7.** Left valve, detail of ligament, cardinal teeth, and posterior lateral tooth. **8.** Detail of cardinal tooth and ligament of a right valve. **9, 10.** Dorsal views of two specimens showing variability in shape and length of the gap between valves. **11.** Inner view of a right valve margin, showing scars of inner radial mantle muscles and anal siphon retractor (arrowhead). Scale bars: Figures 1–7, 11 = 1 mm; Figure 8 = 0.5 mm; Figures 9, 10 = 200μm.

itan (Burch, 1975; Kuiper, 1966, 1983; Kuiper and Hinz, 1984; Holopainen and Kuiper, 1982). However, these specimens are larger than *P. chiquitanum* new species (mean SL from measurements given by the authors was: 4.51 ± 1.31 and maximum shell length: 7 mm), having more central beaks and less produced anterior end. Furthermore, *P. chiquitanum* new species differs from *P. casertanum* in being less convex, with lower and narrower beaks, decidedly located backward. Moreover, *P. chiquitanum* has a comparatively long pre-siphonal suture, being about 11–13% of the shell length, while *P. casertanum* has a shorter one comprising ca. 10% of shell length (Holopainen and Kuiper, 1982; Korniushin, 1996).

Pisidium chiquitanum new species shares with *Pisidium magellanicum* (Dall, 1908) the same siphonal arrangement, the type of nephridia and the number of demibranchs. However, *P. magellanicum*, the only *Pisidium* species from Argentinean and Chilean Patagonia known to have two siphonal openings and two demibranchs, differs from *P. chiquitanum* by the more central position of beaks (mean = 56%, range 53–58% of SL), shorter presiphonal suture, representing about 7.7% of shell length, and shorter ligament (mean = 19%, range: 18–20% of SL) (measurements and indices



Figures 12–14. *Pisidium chiquitanum* new species. **12.** Gross anatomy. **13.** Mantle muscles. **14.** Inner view of inner demibranch. (**bp**, brood pouch; **as**, anal siphon; **ia**, inhalant aperture; **id**, inner demibranch; **irm**, inner radial mantle muscles; **n**, nephridium; **od**, outer demibranch; **pss**, presiphonal suture; **sr**: retractor muscles of siphonal openings). Scale bar 1 mm.

are those reported by Ituarte (1996) and correspond to specimens of *P. magellanicum* from Río Chico, Santa Cruz Province, Argentina studied by Pilsbry (1911) which are part of lot 88811 ANSP).

Pisidium chiquitanum new species chiefly differs from the group of species distributed along the drainages of southwestern Brazil, Uruguay, and northeastern Argentina (Ituarte, 2000) in having two demibranchs and two siphonal openings. Among those, *Pisidium sterkianum* Pilsbry, 1897, a species widely distributed in central and northern South America, also differs from *P. chiquitanum* new species by an evidently external and protruded ligament, having a more inflated shell and nephridia of open type (Korniushin, 1998); *Pisidium dorbignyi* Clessin, 1879, from Uruguay and *Pisidium vile* Pilsbry, 1897, described from Uruguay and also distributed in Bolivia and Argentina are much smaller species; *Pisidium pipoense* Ituarte, 2000, is larger than *P. chiquitanum* new species, having a marked subquadrangular shell outline, while *Pisidium taraguyense* Ituarte, 2000, differs in having a larger and quite globose shell, with fuller beaks. *P. chiquitanum* new species differs from *Pisidium forense* Meier-Brook, 1967, from Minas Gerais, Brazil, by its smaller size, rounded shell outline, lower and less convex shell, and by having a more internal ligament.

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Favorinus elenalexiae, a new species (Opisthobranchia: Aeolidiidae) from the eastern Pacific Ocean

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ABSTRACT

A new species of Nudibranchia, belonging to the genus *Favorinus* Gray, 1850, is described. It differs from other species of that genus mainly by its rhinophoral ornamentation: *Favorinus elenalexiae* new species has three large, overlapping flanges with the upper margins free, like three cups; in almost all the species the rhinophores are papillated or lamellated. The external anatomy, radula, and reproductive system are described and compared with those of other species of the genus. A table comparing summarizing the differences amongst the species of the genus *Favorinus* is included.

Additional key words: Nudibranchia, taxonomy

INTRODUCTION

The genus *Favorinus* includes fourteen species characterized by the presence of a cleioproctic position of the anus. The cerata are arranged in arched clusters, lacking cnidosae, the masticatory edge of the jaws have several rows of denticles and the radular teeth are modified to feed on the eggs of other gastropods. The teeth have very elongate cusp and completely lack or have very reduced denticles. In this paper, a new species of this genus from the eastern Pacific is described and a comparison with other *Favorinus* species is presented.

SYSTEMATICS

Genus *Favorinus* Gray, 1850
Favorinus elenaleixa new species
Figures 1–7, Table 1

Description: *External anatomy:* The body is elongate (figure 1). The largest specimen examined was 15 mm long in distended state. The body has up to 7 ceratal groups on each side. The three anterior groups are horseshoe-shaped, while the rest are oblique rows slightly curved at their distal end (figure 2b). The number of cerata in the clusters was 16, 12, 11, 5, 4, 2, and 2 in a specimen 14.5 mm length. The cerata have a smooth surface. The genital papilla lies on the right side at the level of the first ceratal group. The anus lies on the same side at the level of the second ceratal group. The rhinophores are blunt-tipped and have three large overlapping flanges with the upper margins free in the manner of three cups (figure 2a). On the anterior and posterior surface of the rhinophores there is a thin crest joining the flanges. The oral tentacles are long and cylindrical and the propodial tentacles are long and possess a ventral, longitudinal groove. The foot is relatively broad and the tail is long and pointed.

The background color is translucent white. On the head and back there are fine opaque white dots, which can come together as spots of different sizes, except at the base of the rhinophores and base of the oral tentacles. The oral tentacles are translucent white at the base and opaque white along their upper middle. The rhinophores are dark brown except for their base, which is translucent white and their apexes, which are opaque white. The cerata have white spots distributed on their surface; at the level of the cnidosacs the spots join as an irregular ring around the cerata. Internally to the cerata, the extensions of the digestive gland are pinkish (figure 2c). All the digestive branches of a cluster of cerata are joined at the base of the cluster. The digestive branches are pink in color. The foot is translucent white.

Internal anatomy: Two specimens were dissected, with 14.5 and 15 mm length. Salivary glands were not found. The radulae have 19 and 20 teeth, respectively. All the teeth consist of an arched base with an elongate cusp. Both sides of the cusp are smooth and the apex is sharply pointed (figures 3a; 4). There are no basal denticles. The two jaws are large and amber in color. The masticatory edge is long and curved toward the convex face of the jaw at the outer middle (figure 3b). Along the edge are four or five rows of small conical denticles and a marginal row of long conical denticles (figures 3c, 5).

The reproductive system is illustrated in figure 6. The

Figure 1. *Favorinus elenalexiae* External view.

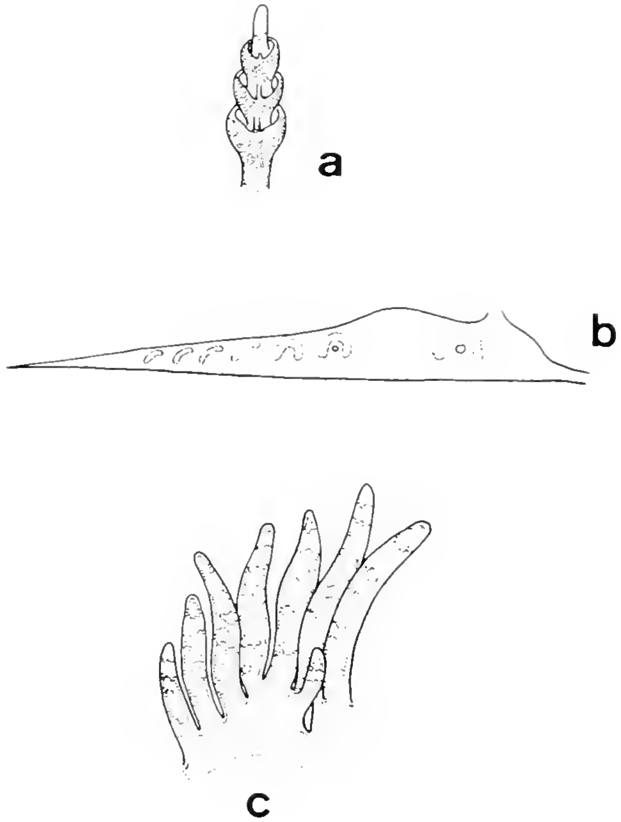

Figure 2. *Favorinus elenalexiae* **a.** Rhinophore **b.** Diagrammatic right profile showing the insertion of the cerata and position of the anus and reproductive apertures **c.** Cerata cluster

gonad empties into a hermaphroditic duct, which enlarges in anterior direction as an ampulla. This is long and coiled, bifurcating at its anterior end into the deferent duct and the inner oviduct. The deferent duct is short; it enlarges into a short prostate, which leads to the penial papilla. Just anterior to the penial papilla, the prostate gives way to a straight post-prostatic duct that connects to the penial papilla. The penis is conical, unarmed, and pointed apically.

The inner oviduct connects to a small and spherical seminal receptacle. The inner oviduct connects to the outer oviduct which penetrates the female gland. This latter is large and envelopes the seminal receptacle. From the female gland the vaginal duct proceeds to the genital orifice.

Type material: Holotype MNCN 15.05/32051, 12 mm length, leg. Francisco J. García, 12 Feb. 1997; Paratype MNCN 15.05/32230, 2 paratypes, 7 and 5 mm length, Isla [illegible], Pacific coast of Panamá, intertidal zone, leg. Francisco J. García, 8 Feb. 1997.

Type locality: Isla [illegible], Pacific coast of Panamá, 3 m depth.

Other material examined: Cuevitas, North of Punta la Gringa, Bahía de los Angeles, Baja California, México, 6 m depth, 1 specimen 6 mm total length, leg. Hans Bertsch, 1 Nov. 1993; South side Isla Cerralvo, Baja California Sur, México, 2 specimens, with egg masses, 5 m depth, 7 June 1985 (one of these used for SEM); Punta de Mita, Nayarit, Mexico, 1 specimen, 9 mm length, 6 m depth, leg. Hans Bertsch, 17 July 1991; Guanacaste, west Costa Rica, 4 specimens, 6 m depth, Leg. Antonio J. Ferreira, 13 Feb. 1972; CASIZ 88218, Islas Ladrones, Pacific Coast of Panamá, 1 specimen, 12.8 m depth, leg. Marty Beals, 13 Apr. 1993; CASIZ 88217, Isla Montuosa, Pacific Coast of Panamá, 12.2 m depth, 1 specimen, leg. Terrence M. Gosliner, 15 Apr. 1993; CASIZ 88135, Isla Jicarita, Pacific Coast of Panamá, 8.83 m depth, 1 specimen, leg. Terrence M. Gosliner, 17 Apr. 1993; CASIZ 88216, Islas Contreras, Pacific Coast of Panamá, 6 m depth, 19 Apr. 1993, 3 specimens, leg. Terrence M. Gosliner; CASIZ 88222, Islas Secas, Pacific Coast of Panamá, 19.2 m depth, 5 specimens, leg. Terrence M. Gosliner, 21 Apr. 1993, CASIZ 97531, Isla Darwin, Galapagos Islands, Ecuador, 18.28 m depth, 1 specimen, leg. Terrence M. Gosliner, 13 May 1994; CASIZ 97510, Isla Isabela, Galapagos Islands, Ecuador, 31.4 m depth, 1 specimen, leg. Terrence M. Gosliner, 14 May 1994; CASIZ 97522, Isla Rabida, Galapagos Islands, Ecuador, 1 specimen, 27.12 m depth, leg. Terrence M. Gosliner, 16 May 1994; Isla Coiba, Pacific coast of Panamá, intertidal zone, 4 specimens 15, 14.5, 5.5,

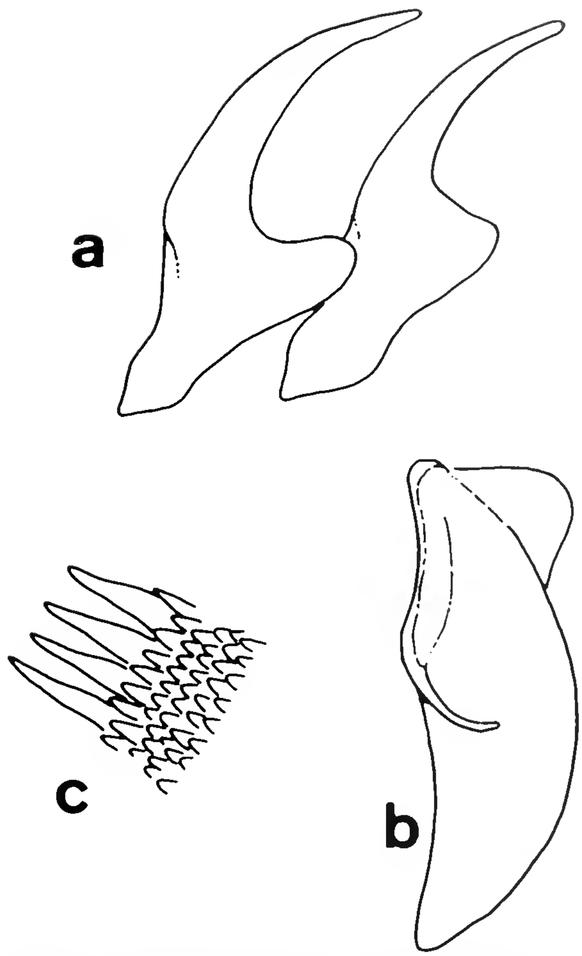

Figure 3. *Favorinus elenalexiae.* **a.** Radular teeth **b.** Jaw **c.** detail of the masticatory edge.

and 3.5, mm in length, leg. Francisco J. García, 8 Feb. 1997.

Distribution (Figure 7): From Bahía de Los Angeles, Baja California, México, to the Pacific coast of Panamá.

Etymology: The name of this species, *elenalexiae*, is a juxtaposition of the names of the youngest daughters of F. J. García and J. S. Troncoso, respectively, Elena and Alexia.

DISCUSSION

The most similar species of *Favorinus elenaleixa* is *F. tsuruganus* Baba and Abe, 1964. This species, described from Japan, was referred to originally as having rhinophores with two bulbs (Baba and Abe, 1964). Later on, however, these authors described the rhinophores as having three cup-shaped flanges (Baba and Abe, 1975), a feature also mentioned in the description of specimens from Eastern Australia by Willan (1983). Willan (*op. cit.*) stated that this character of the rhinophores was known only in *F. tsuruganus*, given that other *Favorinus* species then known have the rhinophores with bulbs along their shaft or are lamellate. Therefore *F. elenalexiae* constitutes the second species of the genus bearing that character.

Favorinus elenalexiae differs from *F. tsuruganus*, however, mainly by its coloration. Although both species have a translucent white ground color and the rhinophores are dark, *F. tsuruganus* has a golden yellow or brownish-yellow head, while that of *F. elenalexiae* is opaque white. The cerata have a deep black cnidosac area and the digestive glands are orange or orange-yellow in *F. tsuruganus*. In *F. elenalexiae*, the cerata have superficial white spots, and a white ring around the base of the cnidosac; and the digestive gland is pinkish. The number of cerata per group is slightly higher in the anterior clusters in our species, while the specimens described by Willan (1983) have more cerata in the posterior clusters. In our specimens the three anterior clusters are arched as a horseshoe, while the rest appear as a more or less curved row. In *F. tsuruganus* almost all are horseshoe-shaped (Baba and Abe, 1975).

Internally, Willan (1983) described the presence of lobe-like salivary glands with a broad duct and a cluster of spherical acini. We did not see any sign of these glands in our specimens. The masticatory edge of the jaws has the outer middle curved toward the convex surface of the jaw in *F. elenalexiae*, while in *F. tsuruganus* it is straight. The radular teeth are similar in both species. The penis of *F. tsuruganus* is u-shaped with the two limbs closely pressed (Willan, 1983). *F. elenalexiae* has a conical penis and it is straight. The internal organs of the reproductive system of *F. tsuruganus* have not been described.

F. elenalexiae has a similar color pattern to *F. mirabilis* Baba, 1955. In both species the rhinophores are dark brown, with the apex whitish; the surface of the notum and cerata are provided by small white spots and the cerata have a general pinkish color. However, other external features distinguish both species. *F. mirabilis* has the rhinophores perfoliated, the cerata set in 12 groups on either side, the general groundcolor is whitish inclined to brown on the back and dorsal surface of the head, the oral tentacles and anterior edge of the foot are yellow, and each cera is marked with a purple spot down the tip. *F. elenalexiae* has the rhinophores with 3 cup-shaped flanges, the body only has up to 7 groups of cerata on either side, the general ground color is whitish with opaque white dots more or less concentrated on the surface of the body, the oral tentacles and foot are white, and the cerata lack a purple spot and have white spots rounding the base of the cnidosac.

In a comparison between *F. elenalexiae* and the rest of the *Favorinus* species, the clearest feature permitting a differentiation is the ornamentation of the rhinophores. Features of the anatomy and coloration of *Favorinus* species are listed and compared in Table 1 making it possible to differentiate *F. elenalexiae* from

Table 1. Characters of species of *Favorinus*

Species	References	Distribution	Rhinophores	Cerata	Body coloration	Rhinophore coloration	Cerata coloration	Radula
F. [illegible]	Present article	Galapagos Island, Eastern Pacific coast of Mexico, Costa Rica and Panama	3 cup-shaped flanges	Smooth	Translucent white with opaque white spots	Black brown with the apex white	White spots on the surface and cnidosac. Digestive gland pink	Smooth
F. branchialis Rathke in Muller 1806	Edmunds & Marcus 1977; Pruvot-Fol 1954; Cattaneo-Vietti et al. 1990	Eastern Atlantic and Mediterranean Sea	1–2 bulbs	Smooth	Translucent white with a variable pattern of opaque white blotches on the back	Brown, tip white	Upper part white opaque. Digestive gland variable: brown, yellow, red, green	Smooth
F. joubini Risbec 1928	Risbec 1953	New Caledonia	Lamallate	NA	Translucent white	Brown with the apex red	NA	8 denticles
F. gouaroi Risbec 1928	Risbec 1953	New Caledonia	2 rings	NA	Yellow with large opaque white spots	Opaque white	Digestive gland yellowish	6 denticles
F. violaceus Risbec 1928	Risbec 1953	New Caledonia	Lamellate	NA	Head yellow greenish, body white with violet glints	Pinkish with the apex violet	White violet	7 denticles
F. pacificus Baba 1937	Baba 1937	Japan	Indistinct constrictions along the whole length	Smooth	Translucent white	Chocolate-tinted except at the distal third which is colorless	Dark yellow with a white cap and a purple marking below	Smooth
F. japonicus Baba 1949	Baba 1949; Baba & Hamatani 1964; Gosliner 1980	Japan, Hawaiian Islands	2 or 3 bulbs	Papillated	Yellowish with dense opaque white except the cerata	Translucent white	Digestive gland red, yellow or yellowish brown, with opaque white apices	Smooth
F. perfoliatus Baba 1949	Baba 1949	Japan	Perfoliated	Smooth	Pale rose	Brown	Digestive gland veined with rose-red	5 denticles
F. mirabilis Baba 1955	Baba 1955; Willan 1983	Japan	Perfoliated	Smooth	Whitish, inclined to brown on the back	Dark brown	Brownish with a purple spot down the tip	Smooth
F. auritulus Marcus 1955	Marcus 1955; Marcus & Marcus 1963; Edmunds 1964; Edmunds & Marcus 1977; Thompson 1980	Tropical west Atlantic	2 or 3 bulbs	Smooth	Translucent white or gray with white spots, the area behind the rhinophores had an orange center	Brown, tip white	White epidermal pigment, digestive gland almost colorless or pink, grayish or dark brown, cnidosac white	Smooth or tiny lateral denticles
F. [illegible] Burn 1962	Burn 1962; Edmunds 1968	Australia	Papillate	Smooth	White	White	Fawn with white tips	NA
F. [illegible] Baba & Abe 1964	Baba & Abe 1964, 1975; Willan 1983	Japan, eastern Australia	2 bulbs or 3 overlapping flanges with their upper margins free	Smooth	Translucent, head golden yellow or brownish yellow, body densely covered with opaque white spots, anterior margin of foot yellowish	Black	White dots down the tip. Cnidosac black. Digestive gland orange	Smooth
F. [illegible]	[illegible]	West Africa, Ghana	3 small swellings	Smooth	Translucent grayish white. A few white dots on head, oral tentacles, back and tail	Tip clear grayish with white dots, the rest purple brown or maroon	A few white dots on surface and a few white glands at tip. Digestive gland cream or brown with purple-brown blotches	7–8 denticles

Table 1. Continued.

Species	References	Distribution	Rhinophores	Cerata	Body coloration	Rhinophores coloration	Cerata coloration	Radula
F. blanus Lemche & Thompson, 1974	Lemche & Thompson (1974); Edmunds & Marcus (1977)	Northern Europe	5 ring shaped swellings	Smooth	Faint straw yellowish and semi hyaline. Shining white pigment on the dorsal side of the oral tentacles continuing backwards between the rhinophores	Yellowish brown	Faint yellowish brown with a narrow almost black strip on the posterior side	Smooth
F. vitreus Ortea, 1982	Ortea (1982)	Canary Islands (Atlantic Ocean)	2 small bulbs	Smooth	Translucent white with opaque white marking on head, dorsum and oral tentacles	White	White opaque	4–5 denticles

NA = Information not available.

the other species by the presence of smooth radular teeth (*F. joubini*, *F. gouaroi*, *F. violaceus*, *F. perfoliatus*, *F. ghanensis*, and *F. vitreus* have denticulate teeth). The radula of *F. pannuceus* Burn, 1962, has not been described. However, this species differs from *F. elenalexiae* by the rhinophores and coloration. The cerata are smooth in *F. elenalexiae* (in *F. japonicus* they are papillated) and the inner oviduct does not have a swelling for a fertilization chamber as was described in *F. japonicus* Baba, 1949 and *F. ghanensis* Edmunds, 1968 (Baba and Hamatani, 1964; Edmunds, 1968). *F. ghanensis* has a small penial stylet.

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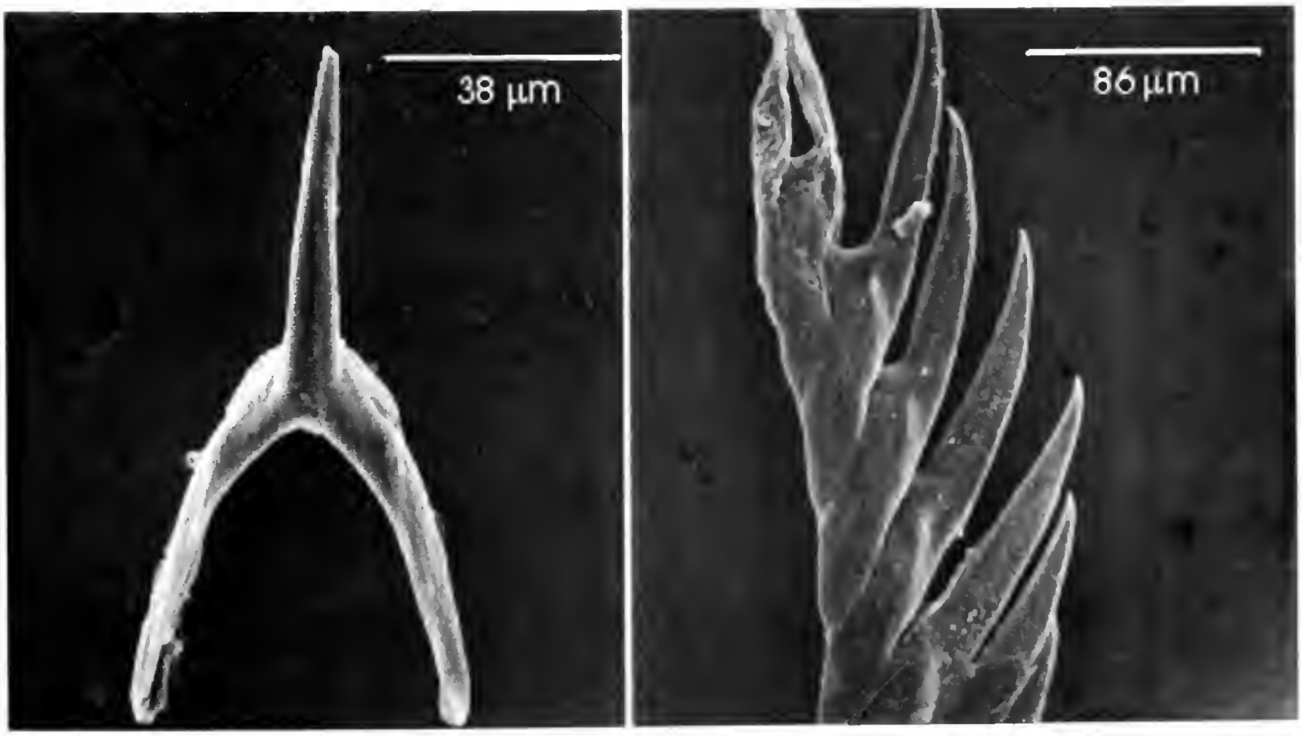

Figure 4. *Favorinus elenalexiae.* Left, SEM micrograph of a radular tooth. Right, SEM micrograph of a lateral view of the radula.

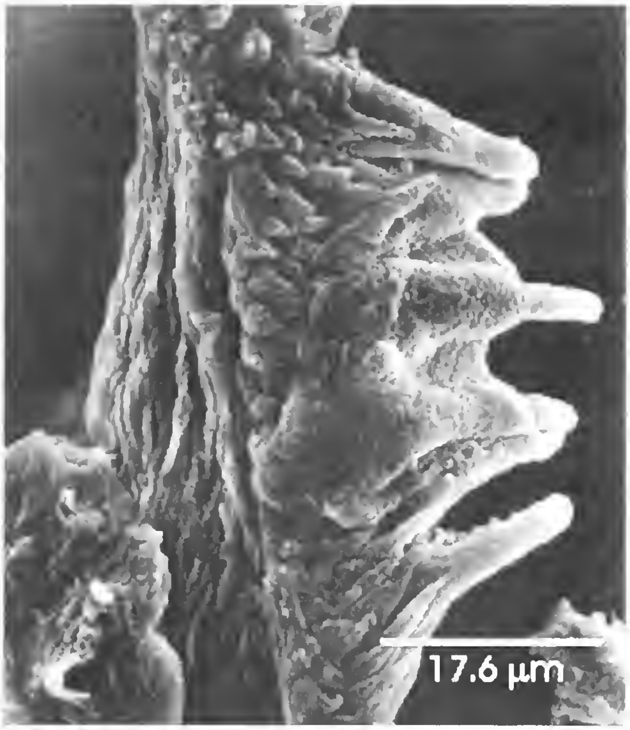

Figure 5. *Favorinus elenalexiae.* SEM micrograph of the masticatory edge of the jaw.

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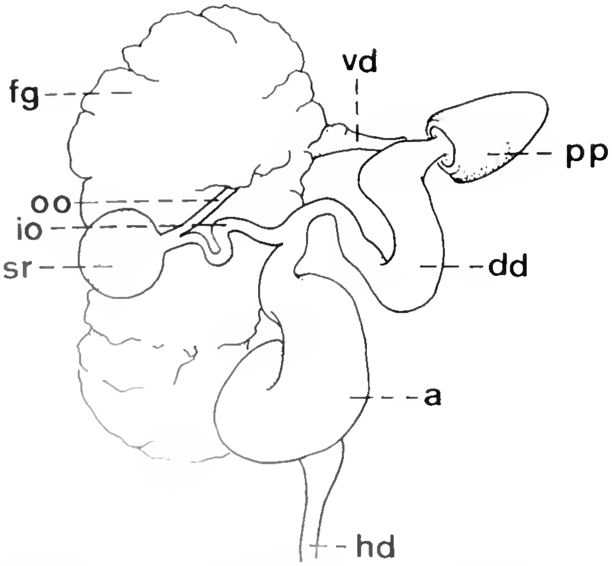

Figure 6. *Favorinus elenalexiae.* Reproductive system. Abbreviations. a, ampulla; dd, deferent duct; fg, female gland; hd, hermaphroditic duct; io, inner oviduct; oo, outer oviduct; pp, penial papilla; sr, seminal receptacle; vd, vaginal duct.

Figure 7. Distribution of *Favorinus elenalexiae.*

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Population dynamics and growth rate of the turbinid gastropod *Lithopoma americanum* (Mollusca) in Biscayne Bay, Florida, USA

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ABSTRACT

The gastropod *Lithopoma americanum* is a common, albeit little-studied, inhabitant of benthic communities from Florida to the West Indies. A survey of *L. americanum* populations was conducted throughout Biscayne Bay, Florida, USA. Abundance of the species was highest in the northeastern portion of the Bay and decreased to zero in the southeastern portion. This pattern may be the result of hydrodynamic and salinity regimes that could prevent the recruitment and survival of larvae in the inner portions of the Bay. Abundance of a population of *L. americanum* at a permanent site within the Bay was monitored for a three-year period, during which gastropod density declined from 26 gastropods m^{-2} to zero. The reasons for this population crash are not clear, but may have been caused by high rates of predation and/or intraspecific competition coupled with a lack of recruitment. Growth rates of *L. americanum* were higher under laboratory conditions (0.46 mm·$week^{-1}$) than in the field (0.25 mm·$week^{-1}$), suggesting that field populations may be food-limited. Growth rate of individuals was also negatively correlated with size.

Additional keywords: Seagrass, ecology, Mollusca, Gastropoda, Turbinidae, *Astraea*

INTRODUCTION

The marine gastropod *Lithopoma americanum* (Gmelin, 1791) (formerly known as *Astraea americanum* and often confused with *Lithopoma tectum* (Lightfoot, 1786)), is found from central Florida, USA, through the West Indies, with occasional, non-reproducing individuals reported as far north as North Carolina, USA (Morris, 1975; Emerson and Jacobson, 1976). *Lithopoma americanum* resides in both soft- and hard-bottom communities, including seagrass beds, rocky shores, and gorgonian/algae-dominated hard-bottom habitats (Hazlett, 1984; McClanahan, 1992). Individuals of this species are most common, however, on seagrasses (*Thalassia testudinum* and *Syringodium filiforme*), where they feed primarily on epiphytic algae (Emerson and Jacobson, 1976; VanMontfrans et al., 1982; Virnstein, 1987; Klumpp et al., 1992; McClanahan, 1992; McClanahan and Muthiga, 1992).

Given the feeding habit of *L. americanum* as a grazer of epiphytes, its feeding activity can have important consequences for the seagrass community. Epiphytes compete with seagrasses for available light, and can potentially reduce the photosynthetic capacity of the seagrass (Howard, 1982; Orth and vanMontfrans, 1984). In such a case, reduction of epiphyte cover by gastropods and other grazers can increase the productivity of the seagrass population, as well as the seagrass community as a whole (Howard, 1982; Howard and Short, 1986; Orth and vanMontfrans, 1984).

Lithopoma americanum is also an important member of the seagrass community as it represents a trophic link between the primary producers and higher-level predators such as crabs, lobsters, and fishes (Randall, 1967; Targett, 1978; McClanahan, 1992). Very little work has been done on *L. americanum*, thus the research presented here proposes to provide basic information on growth rates, population dynamics, and distribution of *L. americanum* populations within Biscayne Bay, southern Florida, USA.

MATERIALS AND METHODS

BISCAYNE BAY SURVEY

The population density of *L. americanum* throughout Biscayne Bay, Florida was quantified at various sites in the bay (figure 1). Most surveys were conducted during the summer of 1998, with additional sites surveyed in the summer of 1999. At each site the number of *L.*

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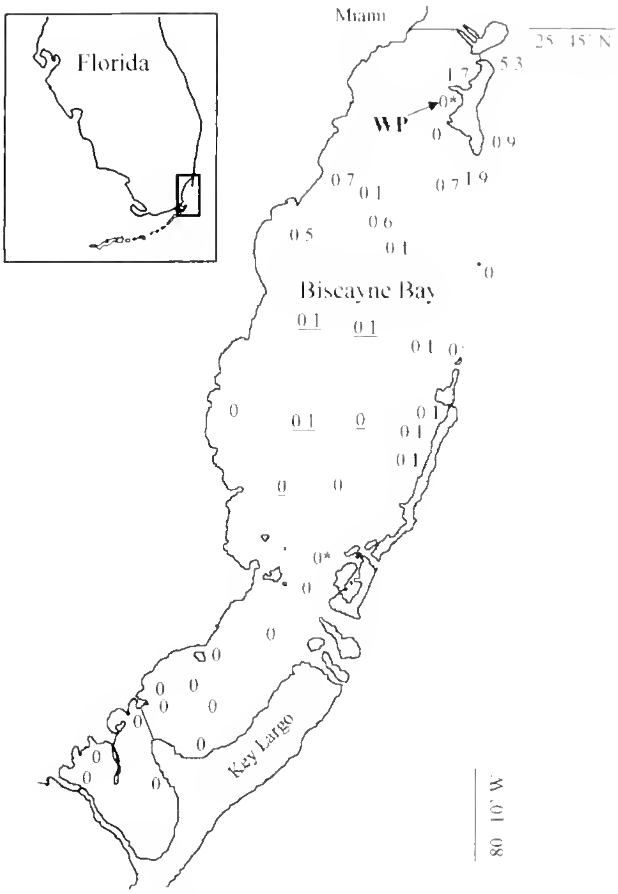

Figure 1. Population density of the gastropod *Lithopoma americanum* at various sites throughout Biscayne Bay, Florida. WP = West Point field site. Numbers indicate the mean number of gastropods$\cdot$m^{-2} at each site. Sites marked 0 had no *L. americanum*, either within or outside of the quadrats. At sites with an asterisk (*), *L. americanum* were present in low numbers but observed only outside of the quadrats. Underlined sites were surveyed in summer 1999, all others surveyed in summer 1998.

americanum was quantified *in situ* with visual censuses of 15 haphazard 1m^2 quadrats. All seagrass blades and drift algal mats within each quadrat were carefully inspected, but this technique may have created a bias against very small individuals. Because the same technique was used for each survey, however, this bias should not affect comparisons among the different sites.

Water depth at each site was measured, and all sites were classified into three depth categories: shallow (0.7–1.5 m), moderate (1.5–2.5 m), and deep (2.5–3.7 m). Sites were also qualitatively classified by substratum into two categories: sparse *Thalassia testudinum* seagrass (approximately < 250 shoots m^{-2}) and dense *T. testudinum* (> 250 shoots m^{-2}). Sites representative of these categories were selected in all regions of the bay (northern, central, and southern), so that there was no overriding geographic pattern to their distribution.

West Point Population Dynamics

Long-term (three years), monitoring of a *L. americanum* population was conducted at a single site (West Point) in northern Biscayne Bay (figure 1). This site is a dense (over 500 shoots m^{-2}) seagrass (*T. testudinum*) bed with depths of 60–180 cm (Maciá, 2000). Monthly surveys were conducted from September 1995 to September 1998. At each survey five parallel 50 m transects were laid out 5 m apart. Gastropods were visually censused *in situ* within a 0.25 m^2 quadrat at five randomly selected points along each transect (except for the first two surveys, in which only 15 and 10 total quadrats [3 and 2 transects], respectively, were counted). As with the above study, there may have been a bias against very small individuals, but this bias should not affect comparisons among the different months. Shell height of gastropods (maximum distance between apex and base of the shell) within the quadrats was also measured with calipers.

Growth Rate Experiments

Twenty-five *L. americanum* were individually marked with a distinct symbol painted on the shell and maintained in an empty outdoor tank (80 × 50 × 40 cm) with a flow-through supply of seawater. Previous attempts at maintaining *L. americanum* in other, larger tanks in which seagrass had been planted indicated that the gastropods remained on the sides of the tanks, feeding on the algae growing there, and did not spend much time on the seagrass itself. Thus, for ease of retrieval of the gastropods, the smaller, empty tank was used for the growth rate experiments.

Shell height of each snail was measured weekly from September 30–December 3, 1998. Snails were classified into 4 size classes: 10.1–15 mm, 15.1–20 mm, 25.1–30 mm, and 30.1–35 mm (no snails in the 20–25 mm size class could be found in the field at the time of this experiment). Some marked gastropods died or were lost during the course of the study. Only those individuals for which at least 4 consecutive weekly measurements were available were used in the analyses. As a result of these losses, and because very few individuals of the larger size classes could be found at the initiation of the experiment, the following are the final number of snails measured in each size class, respectively: 13, 5, 4, 2. All available weekly growth increments were averaged for each individual, and these values were used to calculate a mean growth rate (mm$\cdot$week^{-1}) for each size category.

RESULTS

Biscayne Bay Survey

Individuals of *Lithopoma americanum* were most common in the northern part of Biscayne Bay (figure 1). Sites marked with a 0 in figure 1 represent sites in which no snails were observed either in the quadrats or in the surrounding area while swimming about the site. Two

Table 1. Analysis of *Lithopoma americanum* abundance at various sites throughout Biscayne Bay, Florida. Assumptions of normality and homoscedasticity were not met, thus the data were analyzed with the nonparametric Scheirer-Ray-Hare extension of the Kruskal-Wallis test.

Source	df	MS	F	p
water depth	2	339.44	3.98	0.029
substratum	1	350.94	4.12	0.050
depth*substratum	2	200.66	2.36	0.118
error	34	85.11		

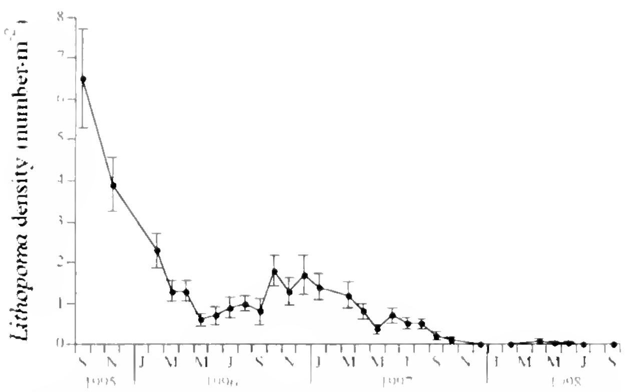

Figure 2. Abundance (mean ± SE) of a *Lithopoma americanum* population at the West Point field site in Biscayne Bay, Florida, from September 1995 to September 1998.

sites (marked 0°) had *L. americanum* present but in such low density that they did not occur within the quadrats (figure 1). No snails were observed in the extreme southern extensions of the bay. Although the northernmost site sampled had a density of 5.3 gastropods·m^{-2}, most sites had less than 1 gastropod·m^{-2}.

When testing for the effects of water depth and substratum on snail density, neither the assumptions of normality nor homoscedasticity could be met. Thus, the non-parametric Scheirer-Ray-Hare extension of the Kruskal-Wallis test was used in lieu of a parametric two-way ANOVA (Sokal and Rohlf, 1995). The Scheirer-Ray-Hare extension ranks all values (with the lowest value given a rank of 1) and uses the ranks to perform an ANOVA. *Lithopoma americanum* was significantly more abundant at dense seagrass sites (0.5 ± 0.3 (SE) snails·m^{-2}) than at sparse seagrass sites (0.1 ± 0.1 snails·m^{-2}) (table 1).

There was also a significant effect of water depth on snail density (table 1), but this result is equivocal. When using actual abundance data, moderate depth sites had the highest mean abundance (0.42 ± 0.41 snails·m^{-2}), followed by shallow (0.33 ± 0.17 snails·m^{-2}) then deep (0.24 ± 0.09 snails·m^{-2}) sites. When using the rank data, however, the pattern was reversed, with deep sites having the highest mean rank (25.3 ± 2.7), followed by shallow (20.9 ± 3.0) and moderate sites (15.3 ± 2.3). Furthermore, a separate linear regression analysis found no significant correlation between water depth and abundance of *L. americanum* ($p = 0.81$; $r^2 = 0.002$). Thus, no clear relationship between depth and population density of gastropods can be determined from these analyses.

West Point Population Dynamics

The highest abundance observed for *L. americanum* at West Point (6.0 ± 1.2 (SE) gastropods·m^{-2}) was during the first survey in September 1995 (figure 2). Gastropod abundance declined steadily during the subsequent seven months, then remained relatively low (less than 10 gastropods·m^{-2}) for the next two years. On the final two surveys density of *L. americanum* within the quadrats was zero, although a few snails were observed throughout the site.

The highest abundance of gastropods coincided with the smallest mean shell size, 8.0 ± 0.2 mm. Excluding the two surveys when only one gastropod was found (May and June 1998), there was a significant negative correlation between *L. americanum* population density and mean shell height (df = 22; F = 23.80; $p < 0.0001$), with an r^2 value of 0.53.

Mean size of *L. americanum* at the field site increased at a rate of 0.23 mm·week^{-1} from September to November 1995 (increase in mean shell height from 8.0 mm to 9.6 mm in 7 weeks) and 0.27 mm·week^{-1} from November 1995 to March 1996 (increase in mean size from 9.6 mm to 13.9 mm in 16 weeks). During the three years of the study a single recruitment event was observed, occurring between July and October 1996 (figure 3).

Growth Rate Experiments

Growth rate of *L. americanum* maintained in the laboratory was inversely correlated with initial shell height (df = 23; F = 11.38; $p = 0.003$), with an r^2 value of 0.34. Snails in the smallest size category grew at the fastest rate (0.46 ± 0.06 mm·week^{-1}), while snails in the largest size category grew at the slowest rate (0.14 ± 0.01 mm·week^{-1}) (figure 4).

DISCUSSION

The abundance of *Lithopoma americanum* in Biscayne Bay decreased from northeast to southwest, with the greatest abundance of *L. americanum* in the northeastern corner of the bay. No gastropods were found in the southern portion of the bay or along most of its western border. There is no clear explanation for this pattern. Seagrass density and water depth do affect the abundance of snails, but those areas devoid of *L. americanum* included sites with both dense and sparse seagrass, as well as sites in all three depth categories. Thus it appears that these factors alone are not responsible for the observed bay-wide pattern.

Although the western side of Biscayne Bay is subject

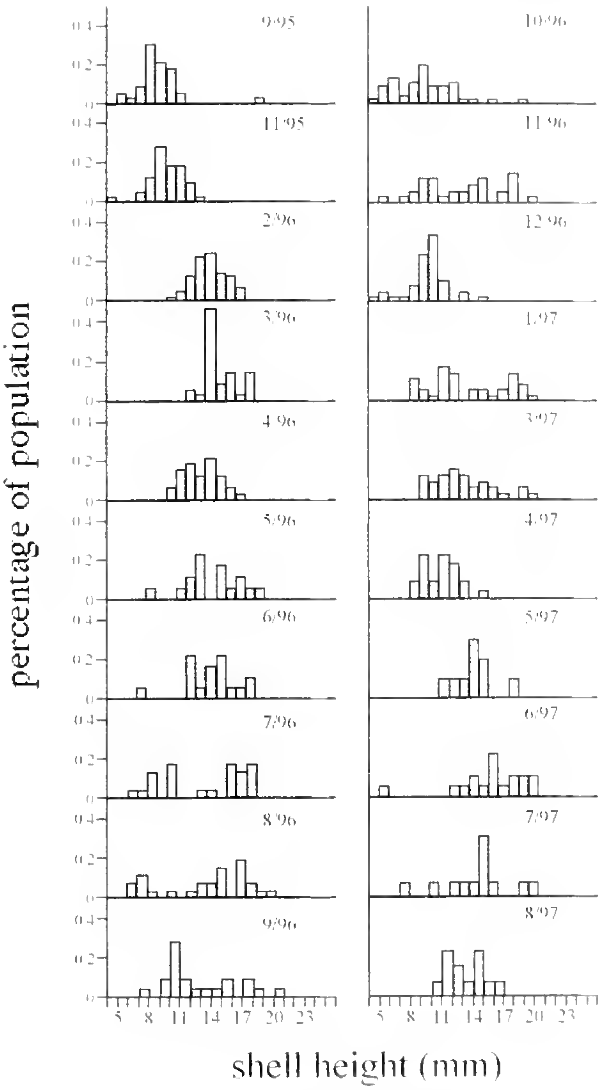

Figure 3. Size frequency distributions for a population of *Lithopoma americanum* in Biscayne Bay, Florida, from September 1995 to August 1997. Population size after August 1997 was too small for meaningful size frequency distributions.

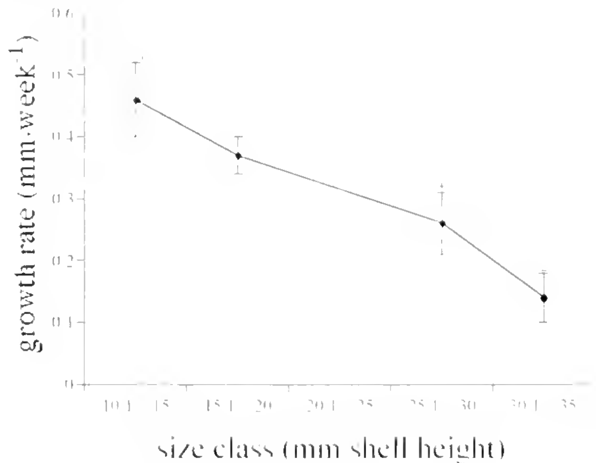

Figure 4. Growth rate (measured as increase in shell height) of *Lithopoma americanum* maintained in the laboratory for at least 3 weeks. Numbers above error bars indicate n for that size category.

to large changes in salinity resulting from freshwater canal discharges from the urban and agricultural areas of Miami (Fatt, 1986; Wang and Cofer-Shabica, 1988), such changes are not a cause of mortality for adult *L. americanum* (Irlandi et al., 1997, identified therein as *L. tectum*). Freshwater discharges to the Bay may not affect adult gastropods, but the larval stages of gastropods and other invertebrates are often much more sensitive to salinity changes (Kinne, 1971). Survival and settlement of larval *L. americanum* may thus be negatively affected in these western areas of Biscayne Bay where salinity fluctuations are most severe (Fatt, 1986; Wang and Cofer-Shabica, 1988).

Recruitment to the inner portions of the Bay may also be limited by the prevailing water circulation patterns. Hydrodynamics in Biscayne Bay are dominated by wind and tide events, which are semidiurnal and change direction into and out of the Bay every six hours (Lee and Rooth, 1971; Swakon and Wang, 1977). When there are no wind-driven circulation effects, direct exchange with oceanic waters is low in the interior and southern parts of the Bay (Lee and Rooth, 1971). If *L. americanum* populations within the Bay depend on larval input from populations outside of the bay to maintain themselves, such hydrodynamic patterns may prevent larvae from reaching the inner bay. This hypothesis is supported by the fact that the site with the highest abundance of *L. americanum* is also the one most exposed to oceanic waters.

The only previously published research on the population dynamics of *Lithopoma americanum* was conducted in the Florida Keys. McClanahan and Muthiga (1992) found *L. americanum* to be the dominant gastropod species in seagrass areas of Florida Bay, with a density of 3.8 gastropods·m^{-2}. Gastropod abundance was also quantified through a second method that measured density as the number of gastropods seen per hour of search time, giving a value of 69.3 gastropods·hour^{-1} (McClanahan and Muthiga, 1992). A previous study covering the same area (McClanahan, 1992) reported a higher density of 200 gastropods·hour^{-1}. Assuming a linear relationship between data collected with the two techniques, the higher value of gastropods·hour^{-1} represents approximately 11 gastropods·m^{-2} for the seagrass habitat.

Maximum density of *L. americanum* in Biscayne Bay, 26 gastropods·m^{-2}, was much higher than that found in Florida Bay. This population density was not sustained for long, however, dropping to 15 gastropods·m^{-2} in just two months, and again to 9 gastropods·m^{-2} within 5 months. Two years later, the abundance of gastropods had declined to nearly zero, and remained so for the duration of the study. A concurrent study at the same

site found no such decline in the local population of sea urchins, *Lytechinus variegatus*, nor was there evidence of any catastrophic changes in water temperature or salinity (Maciá, 2000).

No empty *L. americanum* shells were observed during the study, suggesting that migration out of the site and/or consumption by a predator that destroys the shell were the reasons for the sudden population collapse. In comparison to several other Caribbean gastropod species, however, *L. americanum* has the slowest rates of movement (measured as displacement from an initial location), averaging only 11 cm·day^{-1} (Hazlett, 1984). Thus, movement of the species is relatively slow, and migration out of the site does not appear to be a likely explanation for the rapid drop in abundance of *L. americanum*.

Spiny lobster, crabs, fasciolarid gastropods, and various fishes are potential predators of gastropods such as *L. americanum* (Randall, 1967; Targett, 1978; McClanahan, 1992). The fasciolariid gastropod *Fasciolaria tulipa*, the majid crab *Libinia dubia*, and the pufferfish *Sphoeroides testudineus* were commonly observed at the Biscayne Bay site, and may have been at least partly responsible for the decline in abundance of *L. americanum*. A similar predator-mediated crash in gastropod abundance was reported for a population of *Anachis avara*, another seagrass bed resident found in Biscayne Bay, Florida (Hatfield, 1980). This species demonstrated large seasonal fluctuations in population density as a result of high periodic predation rates as well as seasonal recruitment events (Hatfield, 1980).

Whatever the reason for the initial decline in population size of *L. americanum*, the occurrence of only one significant recruitment event in 3 years is likely to have played an important role in the lack of recovery of the population. A recruitment pulse began in July 1996, reaching its peak in October of that year. This recruitment event was not able to sustain the population, however, as gastropod abundance began to decline steadily after December 1996.

The growth rate of *L. americanum* maintained in outdoor tanks was between 0.14 and 0.46 mm·week^{-1}, with smaller snails growing at a faster rate than larger individuals. The snails at the field site in Biscayne Bay, with a mean size less than 15 mm, grew at approximately 0.25 mm·week^{-1}, much more slowly than the 0.46 mm·week^{-1} observed for similarly sized snails in the lab. This discrepancy suggests that *L. americanum* in the field are food limited. The laboratory-maintained gastropods were feeding on the epiphytic algae growing on the sides of the tanks. These algae may be more abundant or nutritious than those found on the seagrass blades in the Bay, thus providing the snails with a superior food source.

As in the Florida population of *L. americanum* studied here, the congener *L. undosa* (Wood, 1828) from California (USA) also exhibited an inverse relationship between population density and individual gastropod size (Alfaro and Carpenter, 1999). This pattern resulted from intraspecific competition among the snails (Alfaro and Carpenter, 1999). If the quantity or quality of food available to *L. americanum* in Biscayne Bay seagrass beds is poor, as suggested by the growth rate data, the inverse relationship between snail size and abundance may be caused by intraspecific competition. Alternatively, such a relationship could be the result of an unusually successful recruitment event, followed by high levels of mortality (possibly as a result of predation pressure), with the remaining individuals simply continuing on their normal growth trajectory.

Although it appears that intraspecific competition and predation prevent *Lithopoma americanum* from maintaining high population densities, occasionally large but short-lived populations such as the one in Biscayne Bay may temporarily increase the productivity of the seagrass communities in which they reside. Throughout the Bay, *L. americanum* provides a temporally and geographically heterogeneous source of grazing that may release seagrasses from epiphytic competition for light. Snail populations also provide a heterogeneous food resource for higher-level consumers within the seagrass community food web. Overall abundance of *L. americanum* throughout Biscayne Bay is low, but given the abundance of suitable seagrass habitat in the Bay, there exists the potential for successful recruitment events that could affect the populations of both primary producers and higher consumers in the seagrass community.

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Anatomy of *Boonea jadisi* (Olsson and McGinty, 1958) (Heterobranchia: Pyramidellidae) from the western Atlantic, with comparisons to other species in the genus

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ABSTRACT

Boonea jadisi has a thick, conical shell with spiral cords crossed by perpendicular axial ribs, which are absent on the lower half of the body whorl. The smooth, heterostrophic protoconch is oriented 120° to the teleoconch axis and submerged 30–35% within the first adult whorl. Its head-foot, like those of other members of the genus, is translucent and lentiginous, with an unnotched mentum. The tentacles, with tentacular pads, are subtriangular, connate, and ventro-laterally folded. The buccal pump is divided into anterior (bp1) and posterior sections (bp2), with bp2 three times longer than bp1. *Boonea jadisi* is a simultaneous hermaphrodite and produces a non-cuticularized spermatophore. Characteristic features (e.g., alimentary tract configuration) allocate this species, previously included in the genus *Odostomia*, in the genus *Boonea*. A description of the genus and a discussion of the included species are presented.

Additional key words: Functional morphology, systematics, new combination *Odostomia*, Pyramidelloidea, Heterostropha

INTRODUCTION

In 1958, Olsson and McGinty described the species *Odostomia (Chrysallida) jadisi*. This taxon, as well as 533 other species and subspecies included in their work, were obtained "mostly" from Bocas del Toro Island, Panama, Caribbean Sea. It is clear from their records that *O. jadisi* was collected on the island; however, it remains unclear exactly where. The material obtained during their 1953 expedition was from "shore collecting and by the picking of beach drift carefully selected in the field." Later Rios (1970) listed this species from northern Brazil, while van Regteren Altena (1975) collected it in two locations in Suriname. More recently, *O. jadisi* was collected alive at Sebastian Inlet, Florida, USA, which allowed for anatomical study and its allocation in the genus *Boonea*. A description of the genus and species and a discussion of species currently assigned to the genus are provided.

MATERIALS AND METHODS

Specimens of *Boonea jadisi* were collected by scrubbing the undersides of inter- to subtidal rocks. Debris were separated through a series of sieves, the smallest with a mesh size of 0.25 mm. Mud and sand was rinsed off from the material with seawater, and specimens sorted under a dissecting microscope. Living snails were maintained in bowls of aerated seawater. Snails were photographed with a Pentax 35 mm camera mounted on a Zeiss Tessovar dissecting microscope. Shells were cracked with a vise and removed, and snails were dissected whole. Whole animals and alimentary and reproductive systems, before and after excision, were stained with toluidine blue to enhance morphological detail. Line drawings were produced under a Leica MZ8 dissecting microscope with drawing tube. Shells and opercula were cleaned by sonication, air-dried, coated with gold-palladium, and examined under a JEOL JSL 6000 scanning electron microscope set at 5–10 KV. Institutional abbreviations are: ANSP, Academy of Natural Sciences of Philadelphia; USNM, National Museum of Natural History, Smithsonian Institution; HMNS, Houston Museum of Natural Science.

SYSTEMATICS

Family Pyramidellidae Gray, 1840
Subfamily Odostomiinae Pelseener, 1928
Genus *Boonea* Robertson, 1978

Boonea Robertson, 1978: 364. Type species: *Jaminia seminuda* C. B. Adams, 1839, by original designation.

Description: Shell thick, chalky white, conical, 3–6 mm in length, with 3–6 adult whorls. Whorls with or without spiral cords, axial ribs, or combination of both. Body whorl 50–65% of shell length. Umbilicus minute or absent. Smooth, heterostrophic protoconch oriented 120–140° to teleoconch, partially submerged in first adult whorl. Aperture auriform, with single acute columellar fold. Operculum tan or brown, auriform, paucispiral, with subcentric nucleus.

Head-foot white, translucent, and often lentiginous. Foot narrowing posterior to propodium, widening and narrowing again posteriorly to a blunt tip. Posterior pedal gland producing attachment thread. Tentacles subtriangular, connate (= conjoined at tentacular bases, see Wise 1996: p. 455, figs. 21A–C), ventro-laterally folded, tentacular pads present. Eyes subepithelial, on median sides of tentacle bases. Anterior mentum edge unnotched and mentum not bifurcate (= not bisected longitudinally). Introvert-proboscis aperture on ventral side of head, dorsal to mentum base.

Dorsal and ventral ciliated strips joining on mantle roof at posterior end of mantle cavity. Ventral ciliated strip gland composed of mostly white cells, with a few scattered yellow to orange cells, underlying 20–25% of most anterior portion of ventral ciliated strip. Small, oblong pigmented mantle organ (PMO) composed primarily of bright yellow cells, although generally some number of clear, orange, green, brown, or red cells present depending on species. Introvert joining buccal sac, which is composed of sucker, mouth, sheathed stylet with separate opening, oral tube, and stylet bulb. Buccal sac joining buccal pump, which is divided into anterior (bp1) and posterior sections (bp2).

Esophagus originating on ventral surface of bp1-bp2 junction. Salivary gland ducts entering gut and extending parallel to one another within walls of bp1 and entering stylet bulb without exiting alimentary tract. Salivary glands not attached distally to esophagus. Penis globose or small, with rounded anterior and bulbous posterior. Penis located outside and ventral to nerve ring. Noncuticularized spermatophores transferred during mating and usually (although see below) attached to posterior portion of snail's neck (e.g., in *Boonea seminuda*) or deep within mantle cavity on dorsal mantle wall to left of excurrent siphon (e.g., in *B. impressa* and *B. bisuturalis*).

Boonea jadisi (Olsson and McGinty, 1958) new combination (Figures 1–13)

Odostomia (Chrysallida) jadisi Olsson and McGinty, 1958: 43, pl. 1, figs. 11a, 11; Abbott, 1974: 294, no. 3497

Menestho jadisi (Olsson and McGinty, 1958) Odé and Speers, 1972: 7

Chrysallida jadisi (Olsson and McGinty, 1958) van Regteren Altena 1975: 78, figs. 33a, b; Rios, 1994: 187, pl. 61, fig. 87 t.

Material examined: Holotype of *Odostomia (Chrysallida) jadisi* Olsson and McGinty 1958, ANSP 211916. Type locality: Bocas del Toro I., NE Panama, March 1953. Type lot of *Odostomia (Chrysallida) nioba* Dall and Bartsch, 1911, USNM 223284, 7 specimens (a distinct species examined for comparative purposes). Type locality: Bermuda. All specimens for this study were collected at Sebastian Inlet, Florida, USA (27°51.6′ N, 80°26.9′ W), by author under rocks just west of the bridge, on the north side of the inlet (1998–2000). Voucher specimens of *B. jadisi* HMNS Cat. No. 19069.

Taxonomic remarks: DeJong and Coomans (1988) suggested that the species is closely related to *Chrysallida nioba* (Dall and Bartsch, 1911). Examination of the types of this species revealed that this species is conchologically similar to *B. jadisi*. However, as noted by Dall and Bartsch (1911: 286) in their original description, and by DeJong and Coomans (1988), the protoconch, unlike those of most pyramidellids, is scored by spiral grooves. The type lot of *C. nioba* (7 specimens, USNM 223284) contains a specimen, originally designated as the "figured type". However this type was not figured in the original description (Dall and Bartsch, 1911: 286).

Description: *Shell and operculum (Figures 1–8):* Shell white, thick, conical, at least 3.5 mm in length, with 5–6 adult whorls (figures 1, 2, 8). Teleoconch whorls with 4–5 spiral cords parallel to sutures. Cords of upper whorls crossed by perpendicular axial ribs, giving a cancellate appearance (figures 1–3). Intersection of ribs and cords (forming very slight nodes) delineating numerous, fairly deep, generally rectangular depressions. Body whorl approximately 50% of shell length, with only upper one-half of spiral cords crossed by axial ribs. Lower half with only spiral cords, separated by grooves constructed of linear series of irregularly shaped depressions (figures 1, 2). Ovate, auricular aperture with scalloped thick outer lip and fluted base. Recessed, single, acute columellar fold on upper half of columella perpendicular to columellar axis. Smooth, heterostrophic, protoconch oriented 120° to teleoconch axis, submerged 30–35% within first adult whorl, with earliest portion of protoconch partially exposed (figures 4, 5). Operculum brown, auricular, paucispiral, with subcentric nucleus, lacking notch to accommodate columellar fold, and completely closing aperture (figures 6, 7).

Head-foot and visceral mass (Figures 9–10): Head-foot translucent, lentiginous, with scattered white cells. Propodium with very slight medial indentation and rounded antero-lateral edges (figures 9, 10). Foot narrowing posterior to propodium (pd), then widening to gradually taper to blunt apex. Pedal gland (producing attachment thread) within posterior end of deep and long medial groove (pmg) extending from middle to posterior end of ventral surface of foot (figure 10). Tentacles subtriangular, connate, ventro-laterally folded. Tentacular pads present. Eyes widely spaced, black, with lenses beneath epithelium on median sides of tentacles (te). Anterior mentum (me) edge unnotched and not longitudinally bisected (figure 9). Digestive tissue of visceral mass pale orange, yellow brown or light brown, with red flecks.

Alimentary tract (Figure 11): Retracted introvert-proboscis (p) extending posteriorly from its aperture on ventral side of head, dorsal to mentum base, to enter cephalic hemocoel. Proboscis joining buccal sac (bs) that is connected to buccal pump. Buccal pump divided into anterior (bp1) and posterior sections (bp2), with bp2 three times longer than bp1; bp1 round in [illegible]

Table 1. Species assigned to the genus *Boonea* Robertson, 1978. Angle of protoconch inclination (= deviation *sensu* Knight et al. 1960), % submergence within teleoconch and ratios of bp1 and bp2 for seven species of *Boonea*. The gut anatomies of *B. bisuturalis*, *B. kinpana*, and *B. someri* are unknown. NA = Information not available.

Species	Angle (°)	Submergence (%)	bp1 vs. bp2
Boonea bisuturalis (Say, 1822)	120	40–45	NA
B. cincta (Carpenter, 1864)	130	30–35	1.0:1.0
B. impressa (Say, 1822)	130	40–45	3.0:1.0
B. jadisi (Olsson and McGinty, 1958)	120	30–35	1.0:3.0
B. kinpana Hori and Nakamura, 1999	140	50–55	NA
B. okamurai Hori and Okutani, 1996	135	33.3	1.0:1.7
B. seminuda (C.B. Adams, 1839)	120	40–45	51.5:1.0
B. someri (Verrill and Bush, 1900)	130	40–45	NA
B. suoana Hori and Nakamura, 1999	130	30–35	1.0:1.4
B. umboniocola Hori and Okutani, 1995	135	50	2.0:1.0

thickened along last one-third of its length; bp2 wider, somewhat laterally flattened, distally rounded (figure 11). Esophagus (es) elongated, with tuberculate surface, originating on ventral surface of alimentary tract at junction of bp1-bp2. Esophagus extending into visceral mass to join stomach. Salivary gland ducts (sd) entering alimentary tract immediately anterior to bp1-bp2 junction, extending parallel to one another within walls of bp1, and entering stylet bulb (sb) without exiting alimentary tract. Paired salivary glands (sgl) not attached distally to esophagus. Well-developed vesicles (sgltv) forming terminus of each gland.

Pallial cavity: Anterior mantle edge finely plicate, with small, single dark cells at surface and larger, aggregates of white cells just posterior to mantle edge. Dorsal and ventral ciliated strips joining on mantle roof at posterior end of mantle cavity. Ventral ciliated strip gland composed of mostly white cells, with a few scattered yellow or orange cells, underlying 20–25% of most anterior portion of ventral ciliated strip. Small, oblong pigmented mantle organ (PMO) consisting of very dark brown cells suspended in a matrix of mainly yellow cells. PMO releasing thick, bright yellow exudate when snail is disturbed. Kidney suspended from mantle roof immediately posterior to PMO. Pericardial cavity with heart composed of single auricle and ventricle, immediately posterior to kidney at junction of mantle cavity and visceral mass.

Reproductive system (Figure 12): Simultaneous hermaphrodite, with ovary and testis within lobules of single gonad (= ovotestis). Gonad filling concave side of visceral mass. Ovotestis connected to seminal vesicle by narrow hermaphroditic duct. Short duct joins seminal vesicle to coelomic gonoduct. This portion of gonoduct includes fertilization chamber and convergence points of seminal receptacle and albumen, mucous and pallial glands. Reproductive system monaulic. Common pallial gonoduct extending anteriorly beneath mantle floor to open on right side of head, anterior to right tentacular base above dorsum of foot. When retracted, penis lies inside cavity, outside and ventral to nerve ring. Penis with rounded (retracted) to slightly attenuated (protracted) anterior end (atp), widening to ciliated (c), bulbous posterior (bbp) (figure 12). Posterior muscle fibers (mf) attach penis to cavity. Penis extending to outside via medial opening, immediately ventral to mentum. Non-cuticularized spermatophores extruded through gonoduct opening. Spermatophore placement not observed, however, in one individual, it was attached to an operculum (figure 8).

Nervous system: Epiathroid. Nerve ring, including visceral ganglion (but minus osphradial ganglion and buccal ganglia), is highly concentrated and encircles alimentary tract. The outlying osphradial ganglion is connected to supraesophageal by long nerve extending across nerve ring immediately anterior to proboscis. Buccal ganglia attached to surface of primary retractor muscle (figure 11, prm) at distal portion of inverted proboscis.

Ecology and Distribution: *In situ* feeding was not observed, although on several occasions in the laboratory, *B. jadisi* fed quite readily on *Cerithidea costata* (pers. obs.) *Boonea jadisi* occurs from Florida, into Texas and south to Uruguay (Odé and Speers, 1972; Abbott, 1974; Rios, 1994). Rios (1994) reported it on *Sargassum* in Brazil.

DISCUSSION

Robertson (1978, 1996) has argued that shell characteristics provide poor clues for developing hypotheses of

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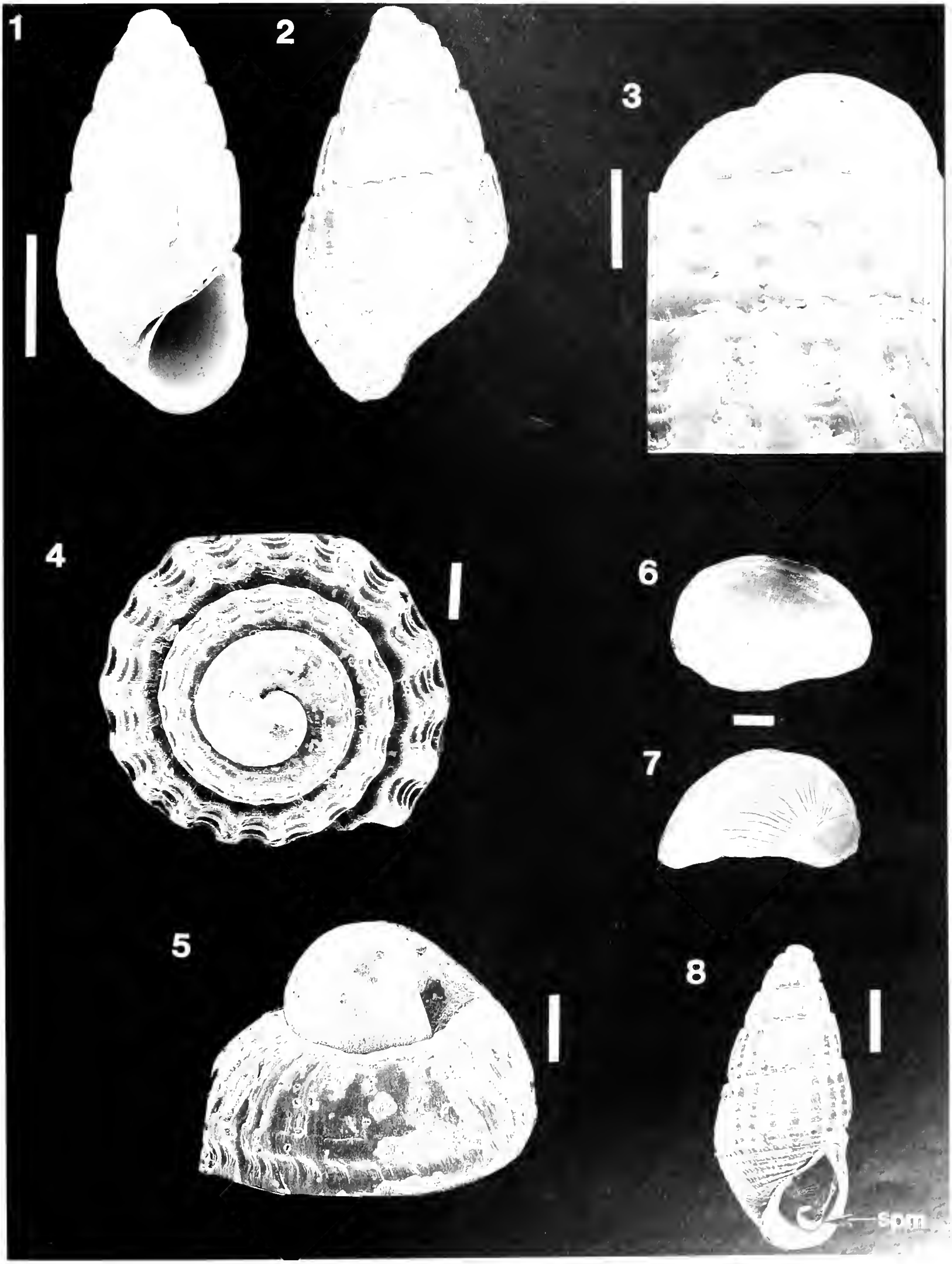
Figures 1–8. Scanning electron microphotographs of shell and operculum of *Boonea jadisi*. **1.** Apertural view. **2.** Dorsal view. Scale bar = 600 µm. **3.** Enlargement of upper portion of teleoconch to reveal detail of shell sculpture. Scale bar = 100 µm. **4.** Apical view of protoconch. Scale bar = 100 µm. **5.** Lateral view of protoconch. Scale bar = 100 µm. **6, 7.** Operculum. **6.** Attachment side. **7.** Unattached side. Scale bar = 100 µm. **8.** Shell with spermatophore attached to operculum. Scale bar = 500 µm. spm = spermatophore.


1
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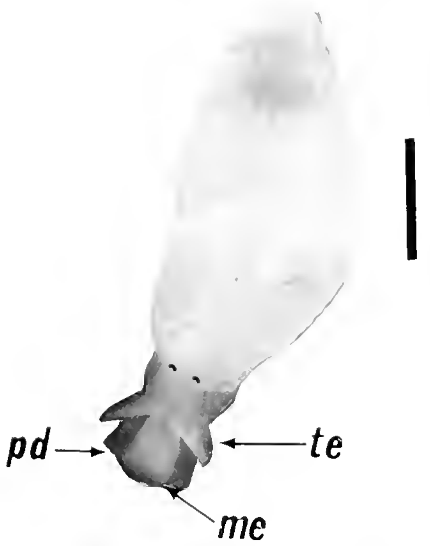


Figure 9. Living *Boonea jadisi*. Scale bar = 1 mm. me = mentum, pd = propodium, te = tentacle.

propinquity within the Pyramidellidae. The pyramidellid genus *Boonea* contains several species with differing interspecific shell morphologies (e.g., *seminuda* vs. *impressa* or *bisuturalis*), including protoconch configurations, as well as interspecific variations in angle of inclination and percent of protoconch submerged within first teleoconch whorl (Table 1). Moreover, it has yet to be sufficiently determined if protoconch morphology is a reflection of phylogeny or developmental mode (for contrasting opinions see Robertson, 1978, and Wise, 1996). Regardless, anatomical studies clearly unite these taxa (Robertson, 1978; Wise, 1993, 1996; Hori and Okutani, 1995, 1996, Hori and Nakamura, 1999). Currently, the anatomies of 7 of the 10 species assigned to the genus are known (Table 1).

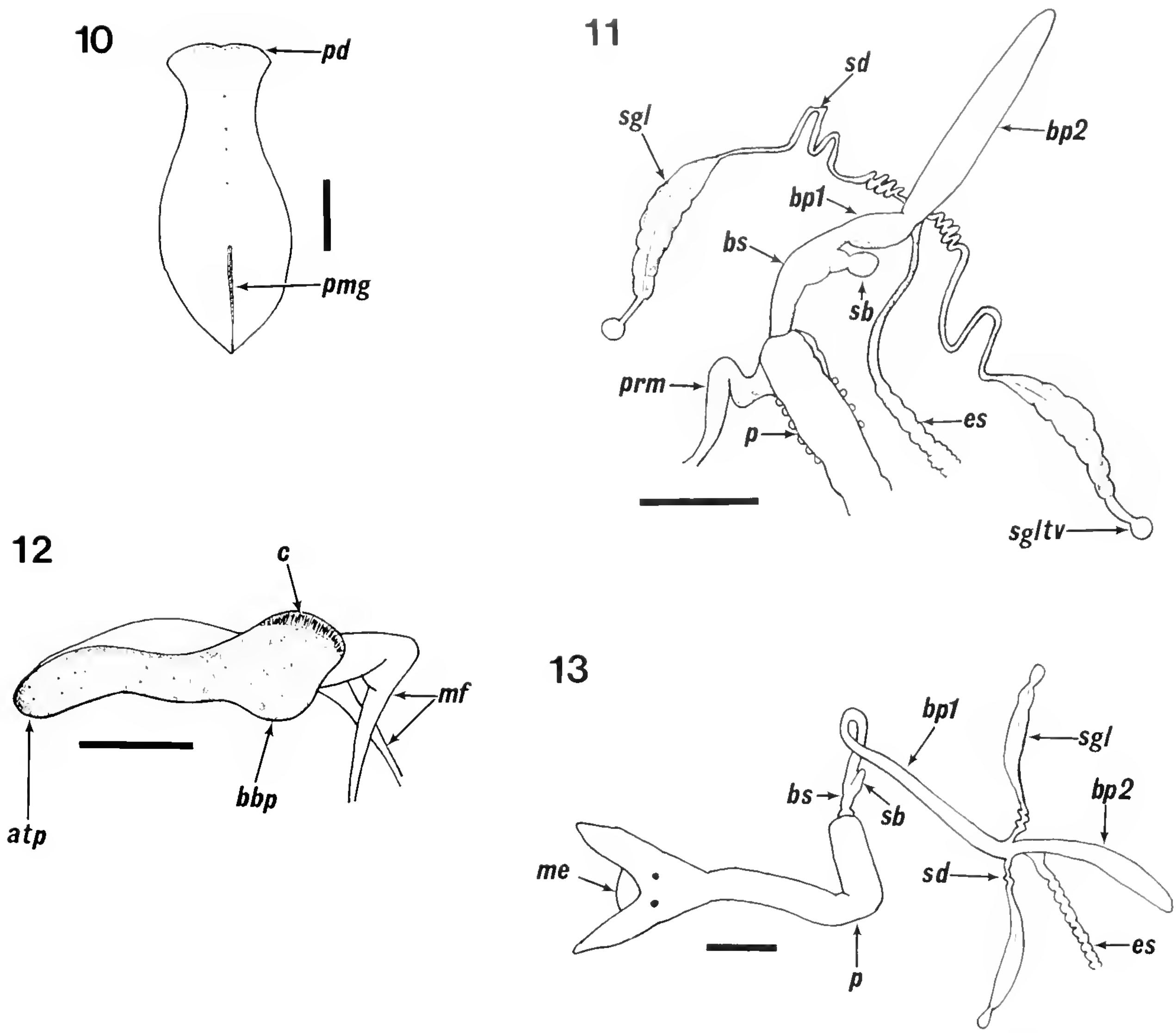
Members of the genus *Boonea* possess apomorphies (e.g., mentum configuration, tentacular pads, and opening of the extrovert/proboscis at the base of the dorsal surface of the mentum) of the subfamily Odostomiinae[1], while a unique gut morphology is an antapomorphy of the genus and its configuration (figure 13) distinguishes this taxon. As in many pyramidellid taxa, the buccal pump is divided into 2 sections, separated by their overall shape and the junction of the esophagus. However, with the exception of the undivided esophagus (e.g., also present in certain species of the genus *Odostomia*) and the interspecific variation in bp1/bp2 ratio (Table 1) the above-described configuration of the buccal pump is diagnostic of the genus (e.g., figures 11 and 13; Hori and Okutani, 1995: fig. 9, 252).

As described for other pyramidellid taxa (Hori and Okutani, 1995; Hori and Nakamura, 1999, Wise 1996; 2000), *Boonea* species have a reproductive tract consisting of a common monaulic, pallial gonoduct, that extends anteriorly beneath the mantle floor to open on the right side of the head anterior to the right tentacular base above the dorsum of the foot. This is contrary to Robertson (1978) who described the "female pore" in Boonea as being on the neck of the snail. The penis, as in the pyramidellid genera *Sayella*, *Houbricka*, and *Pyramidella*, is located in a cavity beneath the mentum, anterior and ventral to the nerve ring. Hori and Nakamura (1999) suggested that because the penial complex was beneath the mentum in *B. suoana* this species must be assigned to the genus *Boonea*. However, as stated above, that arrangement is not unique to this genus. In *Boonea* species, the penis is globose or typically small, with a rounded anterior end that narrows, then widens, becoming large and bulbous posteriorly (Robertson, 1978; Hori and Okutani, 1995, Hori and Nakamura, 1999; Wise, 1996; figure 12). The penis is attached anteriorly and/or posteriorly to the floor of the cavity by muscle fibers and opens to the outside via a medial aperture beneath the mentum.

In *Boonea seminuda*, *B. impressa*, and *B. bisuturalis*, non-cuticularized spermatophores are attached to the dorsal mantle wall to the left of the excurrent siphon, deep in the mantle cavity, half-way between the siphon and anterior end of the mantle cavity or at the neck (Robertson, 1978). In a previous analysis (Wise, 1996: 488), I incorrectly combined the spermatophore attachment preferences in the genera *Fargoa* and *Boonea*. Species of *Fargoa* attach their spermatophores to the shell, typically at the basal disc on the apertural side of the last whorl, posterior and to the right of the posterior end of the aperture (Robertson, 1978). According to Robertson (1978) spermatophores produced by *Boonea* species are small (e.g., in *B. seminuda* and *B. bisuturalis*) to very small (e.g., in *B. impressa*) relative to shell size. All are non-cuticularized, without basal discs, and bulbs near or at the unattached ends. In *B. seminuda*, and only in this species, a lateral spout is present in the spermatophores, while in *B. bisuturalis* and *B. impressa* it is absent. The spermatophores of *B. jadisi* resemble those of *B. bisuturalis* (Robertson, 1978: fig. 12, 370). Spermatophores have not been reported for the other species of *Boonea*.

The nervous system in *Boonea* species (minus the osphradial ganglion and buccal ganglia, but including sub- and supraesophageal ganglia and visceral ganglion) as in other pyramidellids is comprised of a highly concentrat-

[1] Recently Schander et al. (1999) placed *Boonea* in the subfamily Chrysallidinae, family Odostomiidae (wherein they divided the Pyramidelloidea into 6 families and 11 subfamilies). The value of this new classification remains untested, particularly because the authors offered no satisfactory explanation for their enlarged taxonomic scheme. A scheme which follows names proposed by Saurin (1958, 1959), Bronn (1848), and Pelseener (1928) and not unlike these earlier workers, have made this leap without an underpinning of hypotheses of homology based on clearly defined characters and their states. Therefore, for the time being, I choose to work within the admittedly narrower interpretation of the superfamily with only 3 families, one of which, the Pyramidellidae, includes all pyramidellids.



Figures 10–13. *Boonea jadisi.* **10.** Ventral surface of foot. Scale bar = 250 µm. **11.** Alimentary tract. Scale bar = 300 µm. **12.** Diagram of penis. Scale bar = 100 µm. **13.** Head and alimentary tract of *B. seminuda*. Scale bar = 500 µm. atp = anterior end of penis, bbp = bulbous base of penis, bp1 = buccal pump 1, bp2 = buccal pump 2, bs = buccal sac, c = cilia, es = esophagus, me = mentum, mf = muscle fibers; p = proboscis, pd = propodium, pmg = posterior medial groove, prm = primary retractor muscle (attaches at columellar muscle), sb = stylet bulb, sd = salivary gland duct, sgl = salivary gland, sgltv = salivary gland terminal vesicle.

ed ring within the head. The ring encircles the alimentary tract (Huber, 1993; Wise, 1996)). This system is described as epiathroid because the pleural ganglia lie adjacent to the cerebral ganglia. The presence of the osphradium and its ganglion on the snail's left side suggests it euthyneurous condition (= untwisted condition) (Fretter and Graham, 1949; Haszprunar, 1988).

All *Boonea* species are the ectoparasites of a number of invertebrate (mostly molluscan) hosts (Table 2). The genus includes species from the Pacific Ocean (5) and the Atlantic Ocean/Gulf of Mexico (5) (Table 2). Undoubtedly the number of recognizable species of *Boonea* will increase as our understanding of this family improves.

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Table 2. Published information on hosts and geographical ranges for species of *Boonea*

Boonea impressa (Say, 1821): *Crassostrea virginica, Bittiolum varium, Crepidula convexa, Urosalpinx cinerea, Triphora nigrocincta,* "polychaete" worm, *Molgula* sp., *Fargoa* cf. *gibbosa, Geukensia demissa* (Scheltema, 1965; Robertson and Mau-Lastovicka, 1979; Wise, 1993); Massachusetts south to Florida; Texas, USA and Quintana Roo, Mexico.

B. bisuturalis (Say, 1822): *Littorina littorea, Urosalpinx cinerea, Ilyanassa obsoleta, Diastoma alternatum, Nassarius trivittatus, Crepidula fornicata, C. plana, C. convexa, Crassostrea virginica, Mytilus edulis, Mercenaria mercenaria, Argopecten irradians, Crucibulum striatum, Modiolus modiolus, Placopecten magellanicus, Geukensia demissa, Crenella arenaria* (see Robertson and Mau-Lastovicka, 1979); New Brunswick, Canada to New York, USA.

B. seminuda (C. B. Adams, 1839): *Diastoma alternatum, Crepidula fornicata, C. plana, Crassostrea virginica, Mercenaria mercenaria, Argopecten irradians, C. gibbus, Crucibulum striatum, Modiolus modiolus, Placopecten magellanicus, Mytilus edulis, Urosalpinx cinerea, Ilyanassa obsoleta, Nassarius trivittatus* (see Robertson and Mau-Lastovicka, 1979); Prince Edward I., Canada south to Florida; Texas, USA.

B. cincta (Carpenter, 1864): *Astrea undosa, A. gibberosa, Norrisia norrisi, Haliotis* sp. (see LaFollette, 1977); Santa Barbara California, USA, south to Gulf of California, Mexico.

B. jadisi (Olsson and McGinty, 1958): Host *in situ* unknown; in the laboratory-*Cerithidea costata* (this study); Florida, into Texas, USA, and south to Uruguay.

B. someri (Verrill and Bush, 1900): unknown, Bermuda south to Texas, USA (see Odé, 1993).

B. umboniocola Hori and Okutani, 1995: *Umbonium moniliferum,* (see Hori and Okutani, 1995); Tomioka Bay, Kumamoto, Japan.

B. okamurai Hori and Okutani, 1996: *Conus okamotoi, C. sazanka yoshioi, C. flavidus* (see Hori and Okutani, 1996); Okataura Beach, Hachijo Island, Japan.

B. suoana Hori and Nakamura, 1999: *Barbatia virescens* (see Hori and Nakamura, 1999); Yamaguchi Prefecture, Japan.

B. kinpana Hori and Nakamura, 1999: probably *Atrina pectinata* (see Hori and Nakamura, 1999); Yamaguchi Prefecture, Japan.

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Notices

Tables of contents of *The Nautilus* now available online.

The tables of contents of *The Nautilus* are being uploaded into the journal website (www.shellmuseum.org/nautilus_contents.html). We have so far uploaded 60 out of the 115 volumes of the journal. The tables are currently available in html format ("flat" files), but we hope to make the contents (and associated keywords) searchable in the very near future. Please refer to the website for additional information and instructions to authors of *The Nautilus*.

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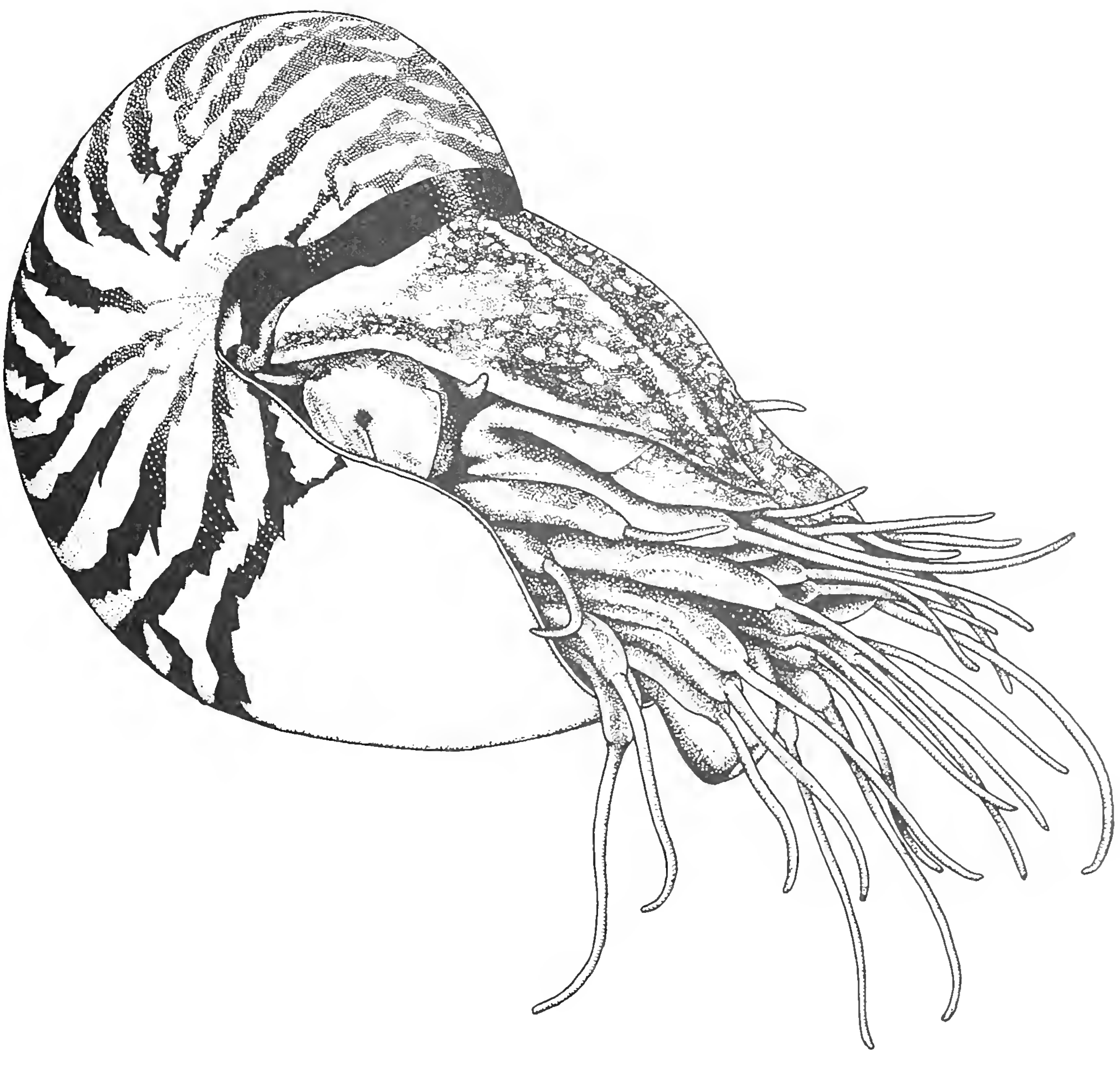

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CONTENTS

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The identity of *Haliotis stomatiaeformis* Reeve, 1846, from the Mediterranean Sea (Gastropoda: Vetigastropoda: Haliotidae)

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ABSTRACT

Haliotis stomatiaeformis Reeve, 1846, is shown to be a senior synonym of *H. neglecta* Philippi, 1848. A lectotype is here designated. Soft parts, radula, habitat, and behavior of the species are described and compared to those of other oblong species with which *H. stomatiaeformis* has been confused in the past. Size at maturity is estimated to be 21.95 mm using shell morphometrics. The species is confirmed as a fourth species in the Mediterranean Sea based on discrete differences in shell morphology and epipodial morphology. The species is restricted to Malta and Sicily.

Additional key words: Gastropoda, Haliotidae, Mediterranean, taxonomy, soft parts, radula, shell, behavior.

INTRODUCTION

The family Haliotidae is a well-known group of gastropods, particularly due to the economic importance of larger species in the seafood industry. Accordingly, the focus of most studies has been on the commercial species found in temperate waters, whereas the tropical abalone species have received less attention. The global treatment of all abalone taxa of Geiger (1998; 1999; 2000), Geiger and Poppe (2000), and Geiger and Groves (1999) has renewed interest in this family. As was to be expected, some of the more tentative conclusions of Geiger (1998) have been confirmed, while others are in need of revision. Here we correct the record of the highly contentious taxon *Haliotis stomatiaeformis* Reeve, 1846, with bearings on a second taxon, *H. neglecta* Philippi, 1848.

The impetus for this reappraisal came from additional material recently obtained by Buzz Owen from four collectors on Malta. This substantially increased the number of known specimens and included six animals. Comparison of this material with the types of *H. stomatiaeformis* by Buzz Owen confirmed his initial suspicion that it is a senior synonym of *H. neglecta*. Here we present detailed arguments and make comparisons with similar species, as well as sympatric species.

MATERIALS AND METHODS

Abbreviations of Collections: BMNH: The Natural History Museum, London; NMW: National Museum of Wales, Cardiff; SBMNH: Santa Barbara Museum of Natural History; USNM: United States National Museum, Smithsonian Institution; BOC: Buzz Owen Collection, Gualala, California; DLG: Daniel L. Geiger Collection, in SBMNH; JKC: Joan Koven Collection, Astrolabe Inc., Silver Spring, Maryland; KAS: Katherine A. Stewart Collection, Carmel Valley, California.

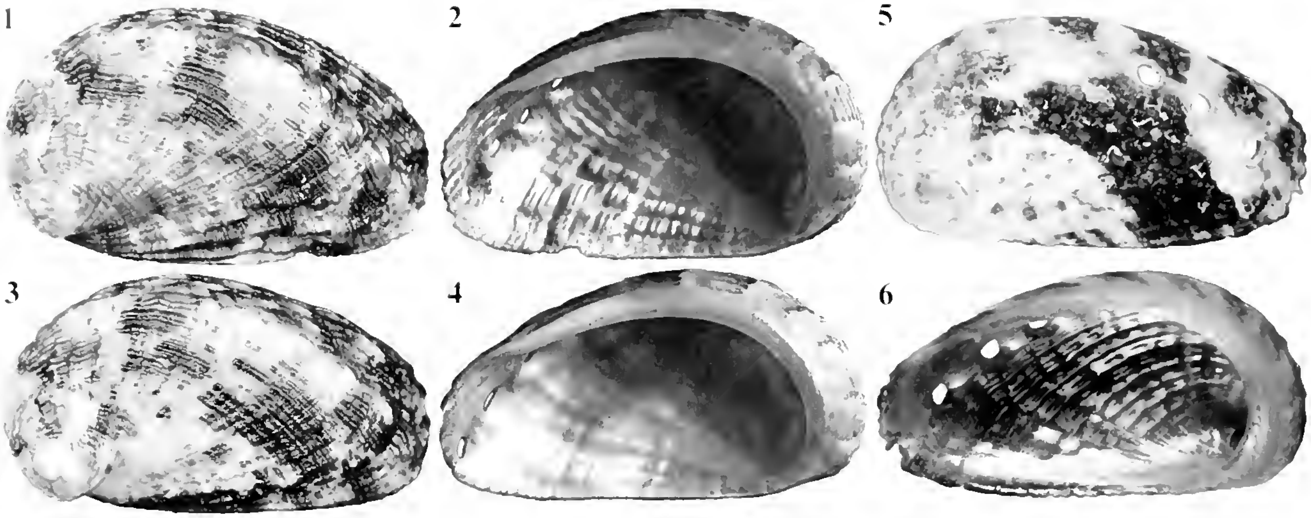
Material Examined: Lots in museum collections are listed in Geiger (1999, 2000) with additional material in BOC. Here we only identify specimens by collection number if relevant. *Haliotis stomatiaeformis*: >200 shells, 6 animals (3 alive in aquarium of A. Wright, Malta), all from Malta; four shells from Catania, Sicily, Italy (leg. Danilo Scuderi, BOC, LACM 152723). *Haliotis tuberculata* Linnaeus, 1758, from the Mediterranean: > 1,000 shells, > 750 animals. *Haliotis squamata* Reeve, 1846: > 250 shells, > 50 animals. *Haliotis dissona* (Iredale, 1929): > 100 shells, 2 dried bodies.

Standard scanning electron microscope (SEM) techniques were employed; for details see Geiger (1996) and Stewart and Geiger (1999). The radula terminology follows that used by Geiger (1996). Statistical analysis was carried out with StatisticaMac 4.1 (Statsoft, 1994).

SYSTEMATICS

Haliotis stomatiaeformis Reeve, 1846
(Figures 1–4, 7–11, 16, 19, 20)

Haliotis stomatiaeformis Reeve, 1846a: 57.—Reeve, 1846b (species 73, fig. 74).—Sowerby, 1882, 26–27, pl. 3, figs 22–23, pl. 11, fig. 113).—Kaicher (1981, 2897, copy of Reeve's figure).—Ubaldi (1993, II 3 2. Listed as unspecified synonym).—Geiger (2000: 63–64, 68, figs. 14, 147, 150).—Geiger and Poppe (2000: 88–89, fig. 71, pl. 2 figs 1–3, 5a–b).—Owen et al. (2001).
not. *Haliotis stomatiaeformis*.—Wagner and Abbott (1978: 00–201) [= *H. varia*].—Talmadge (1963: 134–135, fig 5) [= *H. varia*].—Ostergaard (1935: 7, 34) [*H.* sp.?].



Figures 1–4. Shells of *H. stomatiaeformis.* **1, 2.** Bahar-ic-c'aghaq, Malta, 2–3 m, 6 Nov. 1999, length 24 mm, BOC 15. **3, 4.** Scintu il-Kbir rocks, very close to the tiny islet of Filfla, South of Malta, 2 m taken live, 7 May 1995, length 24 mm, BOC 4. **Figures 5–6.** Shell of *Haliotis dissona.* Site 142, Astrolabe Reef, Fiji, length 17 mm, JKC.

Casto de Elera (1896: 424) [= *H.* sp.].—Pilsbry (1890: 89, pl. 49, figs. 30–35) [= *H.* sp.].—Fischer and Fischer-Piette (1939: 263) [= *H.* sp.].—Habe and Kosuge (1964: 7) [= *H.* sp.].

H. neglecta Philippi (1848: 16).—Philippi (1847–1851: 91–92, pl. 9 figs. 4a, 4b; see Geiger [1998: note 8] for error in figure labeling).—Ubaldi (1987: 285). Reference to species as valid, but not figured.—Ubaldi (1993: 11, 3–1). Listed as unspecified synonym. Geiger (1998: 96–98, figs. 20–21).

Type Material: Three specimens of *H. stomatiaeformis* are deposited in the BMNH (1950.3.16.22–24). One of the specimens (36 mm length) corresponds in size to the one illustrated by Reeve (1846b: pl. 17 fig. 74) and bears a paper label indicating "Type". This specimen (Geiger and Poppe, 2000: pl. 2 fig. 3) is here designated as lectotype; the other two specimens (Geiger and Poppe, 2000: pl. 2 figs. 1, 2) become paralectotypes (shell length 30 mm and 45 mm). All three specimens have a similar coloration and correspond more or less to Reeve's figure.

Discussion of Synonymy: *Haliotis stomatiaeformis* is a senior synonym of *H. neglecta*. The type material in the BMNH consists of specimens of the Mediterranean species known now from Malta and Sicily. The types have several characters in common with recently collected Mediterranean specimens. Direct comparison with the type of *H. neglecta* is not possible, because the whereabouts of the type material consisting of four specimens (Philippi, 1847–1851: 92) is unknown. It could not be located in Bremen, where some of Philippi's material is deposited (J. Lehmann, University of Bremen, pers. comm.). The species is found at the type locality of *H. neglecta* (Sicily) although it is much more common in Malta. Furthermore the two original descriptions (see below) show a number of close similarities, which are indicated by numbers in curly brackets: {1} the overall oval oblong shape of the shell; {2} the convexity of the shell; {3} the spiral sculpture; {4} the fine folds seen in the juvenile part of the shell; {5} the very eccentric spire.

Translation of Original Descriptions:

"Species 73. (Fig. 74, Mus. Cuming.)

Haliotis stomatiaeformis. Shell oblong ovate {1}, very convex {2}, spirally striated {3}, radially finely plicated {4}, spire nearly terminal {5}, elevated; five perforations open; marbled with olive and green.

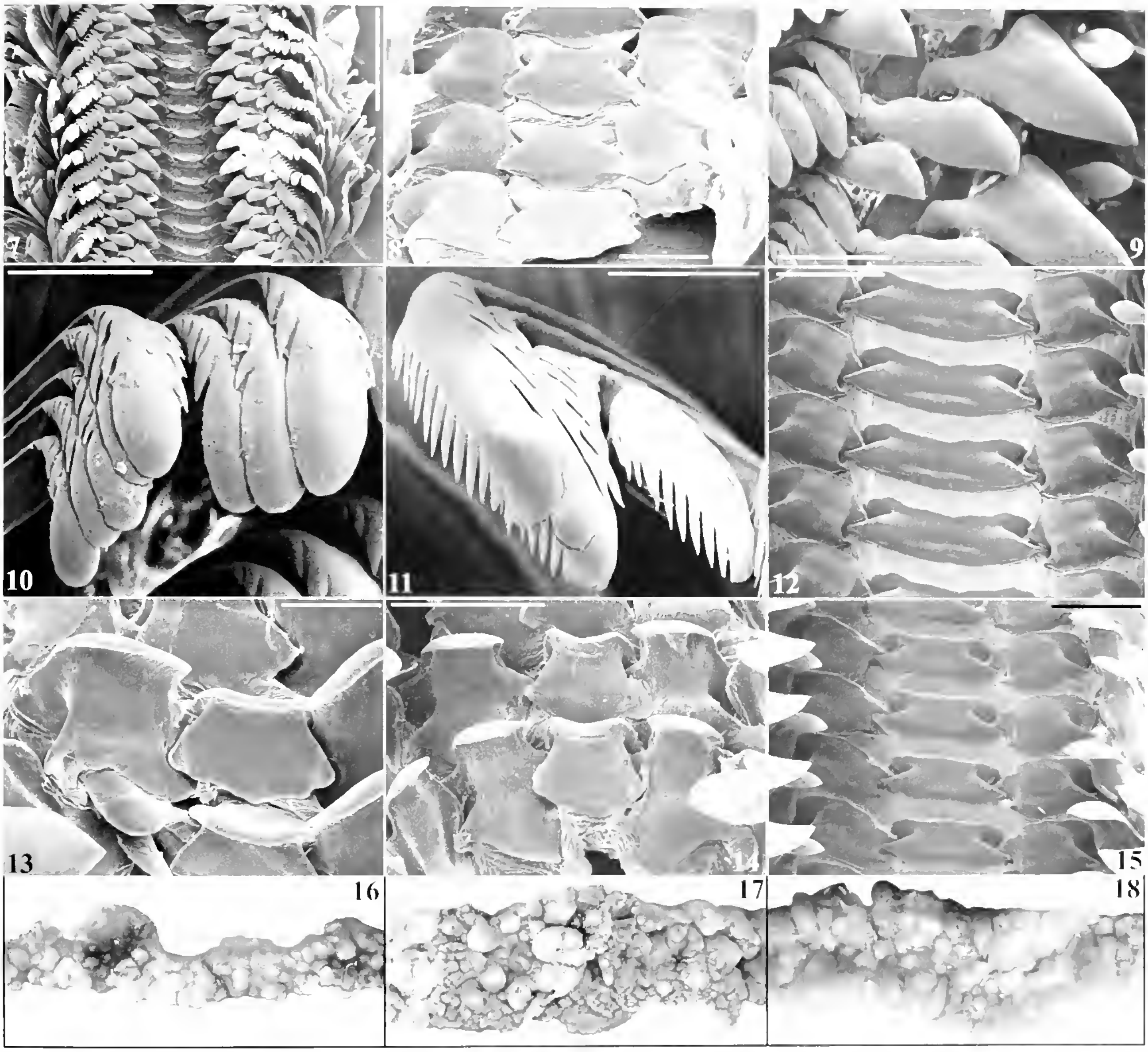
Lives in New Zealand."

"76. *Haliotis neglecta* Ph. *Haliotis* with a oval oblong shell {1}, somewhat convex, with spiral striation {3}, white, with red maculation; with 4–5 open holes; part between the holes and the margin convex {2}; spire small, sideways {5}. Length 11‴; width 6–6.5‴; height 3–3.5‴.

Home: Sicily, rare.

Spiral grooves and ridges approximately 34–32 between spire and holes, approximately 7 between the holes and the margin; little conspicuous, radiating folds finally extinguished towards the spire {1}. Differs from young *H. rugosa* [Lamarck, 1822 or Reeve, 1846?] and *lamellosa* 1) by the more narrow form (*Hal. rugosa* 11‴ long but 7.5‴ wide) 2) by the much smaller spire {5}, 3) by the part between the spire and the holes much more convex {2}, 4) by the part between the spire and the margin similarly convex, not at all grooved, and 5) by the ledge carrying the holes not distinct; and also 6) by the less prominent spire."

Description: Shell (figures 1–4) arched, medium weight or thickness, maximum size 45 mm (paralectotype). Spiral cords smooth, of variable strength, 20–35 between suture and row of holes. One strong cord usu-



Figures 7–15. SEMs of radulae. **7–11.** *Haliotis stomatiaeformis*, BOC. **7.** Overview of radular ribbon, scale bar = 500 µm. **8.** Rachidian and lateral tooth 1. Scale bar = 100 µm. **9.** Lateral teeth 3–5. Scale bar = 100 µm. **10.** Cusps of inner marginal teeth. Scale bar = 50 µm. **11.** Cusps of middle marginal teeth. Scale bar = 20 µm. **12–15.** Rachidian and lateral tooth 1 of some oblong abalone species. **12.** *Haliotis elegans*, USNM 360940. **13.** *Haliotis dissona*, JKC, Astrolabe Reef, Site No. 88, in *Cryptoplax larvaeformis* with coralline algae, February 1995; note sharp angle formed by cutting edge and primary ridge of lateral tooth 1. Scale bar = 50 µm. **14.** *Haliotis glabra*. Note sharp angle formed by cutting edge and primary ridge of lateral tooth 1. Scale bar = 200 µm. **15.** *Haliotis squamata*, SBMNH, East of Cape Preston, Regnard Bay, Western Australia. Scale bar = 200 µm.

Figures 16–18. Representative epipodial section of *Haliotis* spp. **16.** *Haliotis stomatiaeformis*, BOC. **17.** *Haliotis tuberculata*, SBMNH ex DLG. **18.** *Haliotis squamata*, SBMNH.

ally alternating with one to three finer intermediary ones; in < 10% of specimens conspicuous smooth space present between two strong cords; some with adjacent strong cords. Early whorls often with low, irregular, non-colabral folds. Color variable, base color tan, mottled with green, red, brown. Holes slightly elevated, somewhat oblong, usually 3–6 open (mode = 4, Figure 20). First open hole well in anterior half of shell. Spire very eccentric. Interior with steel blue nacre, no muscle scar.

RADULA (Figures 7–11): Rachidian trapezoid, cutting edge neither straight nor folded posteriorly. Lateral tooth 1 triangular, primary ridge more or less straight, secondary ridge inserting at 2/3 of the height. Lateral teeth 3–5 with minor denticles near base of cusp. Inner marginal teeth slightly asymmetrical, first denticle on outer edge at level between first and second denticle of inner edge.

SOFT PARTS (Figure 16): Epipodium very narrow for

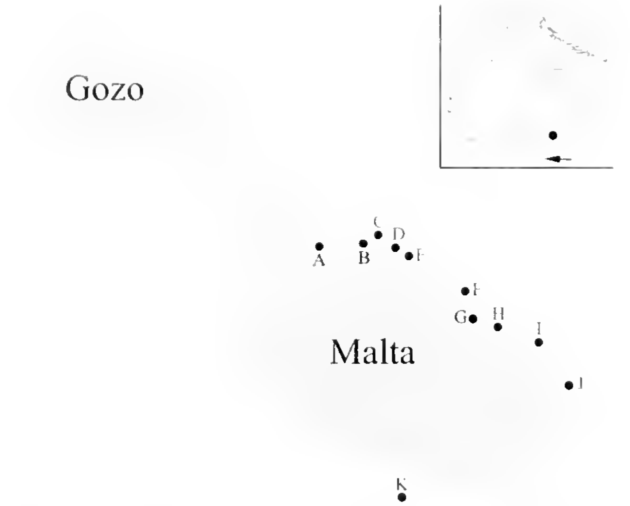


Figure 19. Distribution map and localities of *H. stomatiaeformis*. Numbers in parentheses indicate the number of dead shells/live animals. **A.** St. Pauls Bay (10/0). **B.** Salina Bay (6/0). **C.** Ghallis Rock (7/2). **D.** Qalet Marku (5/0). **E.** Bahar-ic-Caghaq (83/3). **F.** St. Juliens Bay (3/0). **G.** Manoel Island, Gzira (7/0). **H.** Fossa Valletta (7/0). **I.** Xghagra Zabbar (29/0). **J.** Marsaskala Bay (36/0). **K.** Filfla Island (2/1). Inset: Italy with its southern island of Sicily, and marked locality for *H. stomatiaeformis* (Catania: 4/0). Arrow: Malta Island.

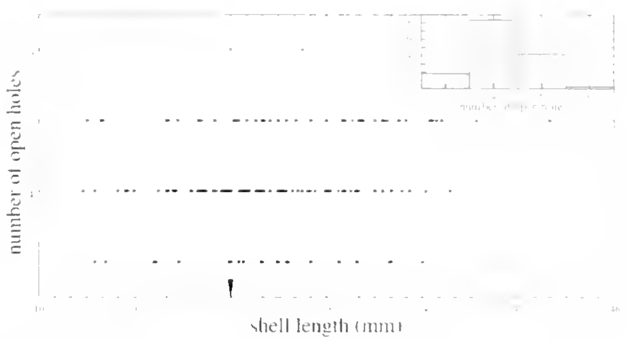


Figure 20. Scatterplot of number of open holes as a function of size (n = 200). Note the slight trend of more open holes with increasing shell size. Breakpoint regression identified the change in slope at 21.95 mm; for shells > 21.95 mm (arrow) the number of open holes does not change with size (p = 0.11). Insert, histogram of number of open holes for shells larger than 21.95 mm: mean = 4.2 (SD = 0.66), mode = 4, n = 146.

genus. Dorsal margin frilled with small projections and bearing large tentacles, at intervals of 2–3 times the width of the epipodium. Face of epipodium with some stubby projections. Ventral side larger than dorsal side, with more numerous, more narrowly spaced, but smaller tentacles. Ventral margin bearing many partially overlapping projections; some projections with bifurcate or trifurcate tips; some small flaps further below. Hypobranchial gland with simple lamellae.

Distribution: Malta and Sicily (Philippi, 1848; 1847–1851; Geiger, 2000; this study: figure 19).

Habitat: Six specimens were taken alive in 1–2 m depth from the underside of flat limestone rocks with a diameter of less than 20 cm on a bottom of gravel and small stones at least 10–15 m from the nearest seagrass (*Posidonia oceanica* [Linnaeus, 1813] Delile). Larger rocks of up to 1 m in diameter did not harbor any specimens. Dead shells were most frequently found at a depth of 2–4 m, to a maximum of 15 m. Shells from deeper water are frequently of reddish color.

Biology: Some behavioral observations were made in aquariums. The species is very active at night, fast moving, and very light sensitive. It moves much faster and is more light sensitive than *H. tuberculata*. Whereas *H. tuberculata* will initially clamp down when disturbed, *H. stomatiaeformis* immediately crawls away rapidly. *Haliotis tuberculata* is regularly found in the open at night, whereas *H. stomatiaeformis* is almost always cryptic. The behavior of *H. stomatiaeformis* is very similar to that of a recently decribed species of *Haliotis* (Owen et al. 2001). One specimen of *H. stomatiaeformis* grew from approximately 25 mm to approximately 35 mm in one year.

We were able to estimate size at maturity from shell morphological data, namely length and the number of open holes. Breakpoint regression analysis on data from *H. tuberculata* has shown that the breakpoint for these two variables corresponds closely with published size at maturity as determined from gonad studies (Geiger, 1998). As in *H. tuberculata*, in *H. stomatiaeformis* there is an a weak trend to increase the number of open holes with size (m = 0.13), although linear regression analysis was only marginally significant ($r^2 = 0.016$, $F_{1,198} = 3.24$, $p = 0.073$, $n = 200$) over the available size range (13.5–42.0 mm). Breakpoint regression analysis with Quasi-Newton loss function ($r^2 = 0.72$) determined the breakpoint to be at 21.95 mm (figure 20), which is taken as the best estimator of size at maturity. Linear regression analysis for specimens larger than 21.95 mm is insignificant ($r^2 = 0.017$, $F_{1,144} = 2.54$, $p = 0.11$, $n = 146$) with a mean number of open holes of 4.2 (SD = 0.66; figure 20). *Haliotis stomatiaeformis* matures at a considerably smaller size than *H. tuberculata* (33 mm), but both mature at approximately half their maximum size.

Remarks: DNA sequence data of the Histone 3 gene fragment confirm that *H. stomatiaeformis* is distinct from *H. tuberculata*; the 328 bp fragment shows 23 discrete differences. Interspecific variation between other species pairs of *Haliotis* sp. ranges from 12 to 24. No intraspecific variation was detected in similar DNA sequences of three specimens of *H. rubiginosa* Reeve, 1846, and two specimens of *H. varia* Linnaeus, 1758, (Geiger, unpubl. data.).

DISCUSSION

Comparisons: *Haliotis dissona* (Figures 5–6, 13): This Western Pacific species is distributed from the Marianas,

Micronesia, New Caledonia, to Tonga. Its spiral cords are much coarser and their number between the suture and the row of tremata is approximately 12, compared to > 20 in *H. stomatiaeformis*. The number of open holes is approximately the same in *H. dissona* (4–5) and *H. stomatiaeformis* (3–6, mode = 4). The coloration is off-white with large, irregular colored areas in brown, red, and green tones. Further illustrations of the species can be found in Kaicher (1981), Geiger (1998, 2000) and Geiger and Poppe (2000).

RADULA (Figure 13): The radula shows the strongly angular lateral tooth 1 seen in some other Indo-Pacific species, such as *H. varia* and *H. glabra* Gmelin, 1791 (cf. Geiger, 1999, figure 14). The epipodium and hypobranchial gland are currently unknown; the two dried specimens did not allow their assessment.

Haliotis squamata: Found predominantly in Western Australia, but additional specimens from Vietnam and Indonesia have come to light in recent years (Geiger, 2000; D. Reid, pers. comm.; A. Thompson, pers. comm.). It is much larger (7–8 cm) than *H. stomatiaeformis* (4.5 cm). Compared to *H. stomatiaeformis*, the spiral cords of Indo-Pacific specimens of *H. squamata* are somewhat stronger, and very much stronger in Western Australian specimens of *H. squamata*, which even bear coarse scales. The number of holes is much greater (6–9, mode = 8) as compared to *H. stomatiaeformis* (3–6, mode = 4). The first open hole of *H. squamata* lies well in the posterior part of the shell, whereas in *H. stomatiaeformis* it is found in the anterior half. The color is usually uniform dark reddish brown to sepia. Irregular folds in the early whorl are only known from one specimen from Indonesia (DLG AAB 13g). In most specimens the concentric sculpture is confined to stronger growth lines. The species has been illustrated in Hinton (1978), Eisenberg (1981), Kaicher (1981), Wells and Bryce (1985), Dharma (1988), Wilson (1993), Geiger (2000), and Geiger and Poppe (2000).

RADULA (Figure 15): The central field is similar to that of *H. stomatiaeformis*. Lateral teeth 3–5 do not bear denticles. The denticles on the marginal teeth are symmetrical.

EPIPODIUM (Figure 18): *Haliotis squamata* and *H. stomatiaeformis* both have a rather narrow epipodium. In *H. squamata* the dorsal tentacles are separated by less than the width of the distended epipodium, whereas in *H. stomatiaeformis* they are separated by 2–3 times the width of the epipodium. The dorsal margin bears finely digitate processes on a knobbed, broad fold. The face of the epipodium is strongly knobbed. The ventral half is wider than the dorsal half. It bears somewhat smaller and more narrowly spaced ventral tentacles and the same digitate processes as the dorsal margin.

Haliotis tuberculata (Mediterranean form): *Haliotis stomatiaeformis* is more elongated, and much more arched. The irregular radial folds are much weaker than in the lamellate forms of *H. tuberculata*. The number of open holes (3–9, mode = 5) and the placement of the first open hole in the anterior half of the shell are very similar to *H. stomatiaeformis*. The elevation of the spire is variable (cf. Geiger, 2000, figs. 12, 13), but the spire is more or less perpendicular to the plane of the shell, and in a more central position on the shell.

Weinkauff (1883:74, translation) noted in his discussion of *H. zealandica* Reeve, 1846 (= *H. tuberculata* Linnaeus, 1758): "Sowerby united with his *H. stomatiaeformis* a small beach form of *H. tuberculata* from Malta with highly elevated spire, which Philippi had called *H. neglecta*. Specimens with monstrously elevated spire are not at all rare in the Mediterranean, and have been known for a long time." Weinkauff was certainly correct in pointing to the high spired forms of *H. tuberculata* from the Mediterranean (cf. Geiger, 2000, fig. 13). However, *H. stomatiaefomis* is not distinguished by the high spire, but by the arched shell, and the rather eccentric spire. *Haliotis tuberculata* has been illustrated in Kaicher (1981, as *H. lamellosa*), Abbott and Dance (1983), Ubaldi (1987), Poppe and Goto (1991), Geiger (2000), Geiger and Poppe (2000), and Owen et al. (2001).

RADULA: Rachidian tooth trapezoid, cutting edge convex without thickening. Lateral tooth 1 primary ridge without concave depression, secondary ridge smaller than primary ridge, inserting at 2/3 of the height of the tooth. Lateral teeth 3–5 without denticles. The marginal teeth show symmetrical denticles on cusp.

EPIPODIUM (Figure 17): The epipodium is of moderate width, i.e., much wider than in *H. stomatiaeformis*. The dorsal margin bears relatively small tentacles, barely extending beyond the margin of the leafy small flaps. The small flaps bear primary and secondary undulations and have a furrowed surface towards the face of the epipodium. The undulating mid-epipodial fold is well developed. The face bears papillae 1–4 mm long at varying densities. The ventral portion of the epipodium is larger and mirrors in structure the dorsal half. Some small tentacles are nested within the furrowed part of the ventral portion.

History: The confusion surrounding *H. stomatiaeformis* may be attributable to the illustration by Reeve (1846b), which does not show enough detail, and the undoubtedly erroneous type locality "New Zealand" (cf. Talmadge, 1963). Three species are known from well-studied New Zealand (*H. australis* Gmelin, 1791, *H. iris* Gmelin, 1791, *H. virginea* Gmelin, 1791) and are all endemic to the island group (Geiger, 2000), and the name *H. stomatiaeformis* has never again been reported from this area. Talmadge (1963:135) recognized the erroneous type locality of *H. stomatiaeformis* (New Zealand) and designated a new one in the Indo-Pacific: "North coast of Java, Indonesia." In doing so he inadvertently added to the confusion. For the most part, *H. stomatiaeformis* has been overlooked, or it has been variously synonymized. Where it has been used, it referred to a number of different species. We provide a brief synopsis of the various applications of the name, arranged by species

that we think was most likely at hand; our identifications of these records are often very tentative, because neither voucher material nor illustrations were available:

Haliotis dissona (Iredale, 1929)—Ostergaard (1935, 7 [as *stomatifomis*], 34 [as *stomataeformis*]), referring to specimens from Tonga, noted (p. 34): "Reeve remarks that this species is well distinguished by its conspicuous convex oblong form." This makes an identification as *H. dissona* very likely.

Haliotis exigua Dunker, 1863—Casto de Elera (1896) made reference to a Philippine species and gave *H. exigua* Dunker, 1863, another controversial taxon (cf. Geiger, 1998), as a synonym. Pilsbry (1890) synonymized *H. exigua* as used by some authors under *H. stomatiaeformis*, and grouped *H. squamata* with *H. stomatiaeformis*. The material Pilsbry (1890) based his treatment on came from New Caledonia and Tonga, and was in the 3 cm range. The description, the size of the specimen, and Pilsbry's pl. 3, fig. 4, make it likely that he was discussing *H. clathrata* Reeve, 1846. However, pl. 49, figs. 30–35 of Pilsbry (1890), show quite a different species.

Haliotis squamata Reeve, 1846—Specimens labeled *H. stomatiaeformis* in the BMNH supposedly from the Solomon Islands and NMW from Viti Levu, Fiji, actually represent *H. squamata*. Geiger (1998) synonymized *H. stomatiaeformis* under *H. squamata*.

Haliotis varia Linnaeus, 1758—Some more elongated specimens of the hypervariable *H. varia* were separated by Talmadge (1963: 134–135, fig. 5) as a distinct subspecies, *H. varia stomatiaeformis*, an opinion followed by Lindberg (1992). Wagner and Abbott (1978) considered the two taxa synonymous.

Unknown species—Fischer and Fischer-Piette (1939) mentioned a specimen from Tanna, Vanuatu. It may either refer to *H. dissona* or to *H. clathrata*. Habe and Kosuge (1964) synonymized under *H. stomatiaeformis* three distinct species: *H. hanleyi* Ancey, 1881 (= *H. jacnensis* Reeve, 1846); *H. planata* Sowerby, 1882, and *H. crebrisculpta* Sowerby, 1914. We are unable to even guess what species was discussed. Ubaldi considered *H. stomatiaeformis* either a valid species from the European-Mediterranean area (1987) or a synonym of a taxon that was not specified (1993).

Sowerby (1882) on the other hand, expressed in a now vindicated renegade opinion, that *H. neglecta* Philippi, 1848, is either a synonym (p. 26–27: "The variety figured in our last plate represents *H. neglecta* Philippi, and is undoubtedly identical with our present species [*H. stomatiaeformis*]") or a variety (caption for pl. 14: "113. *H. stomatiaeformis*, Rve. var. *neglecta*, Ph. See f. 22, 23. Malta") of *H. stomatiaeformis*. *Haliotis neglecta* is itself an overlooked taxon, which was tentatively resurrected as a valid species by Geiger (1998) based on seven shells from Malta. We are now in possession of additional material, including animals, which allows us to conclude that *H. stomatiaeformis* and *H. neglecta* represent the same biological species from the island of Malta and Sicily in the Mediterranean Sea, and thus to confirm the existence of a fourth abalone species in the Mediterranean (*H. tuberculata*; *H. pustulata* Reeve, 1846; *Haliotis mykonosensis* Owen et al., 2001).

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Erratum

In the article by Wise (2001), please correct the ratio bp1/bp2 for *Boonea seminuda* (Table 1, 7th line). The ratio should be 1.5:1.0, not 51.5:1.0 as originally stated.

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Austrodaphnella yemenensis new species (Gastropoda: Turridae) from Yemen, Red Sea, with notes on *A. alcestis* (Melvill, 1906)

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ABSTRACT

The genus *Austrodaphnella* Laseron, 1954, previously known only from Australian waters, is here reported from the Arabian Peninsula. Two species occur: *A. yemenensis* new species, from Yemen, Southern Red Sea, and *A. alcestis* (Melvill, 1906) new combination, a deep water species known only from the Gulf of Oman. SEM photographs of both species are provided.

Additional key words: Indo-Pacific, new combination

INTRODUCTION

This paper deals with the genus *Austrodaphnella* Laseron, 1954, formerly reported only from Australian waters, but here shown also to occur off the Arabian Peninsula. At least two species occur also in the Arabian region, namely *A. yemenensis* new species from Yemen, Southern Red Sea, and *A. alcestis* (Melvill, 1906) new combination, a deeper-water species from the Gulf of Oman.

Austrodaphnella yemenensis is presently known only from a few adult specimens and fragments which were dredged on the continental shelf of Yemen by the French oceanographic ship MARION DUFRESNE, within the frame of the European Community project RED SED '92 (Southern Red Sea and Gulf of Aden).

SEM micrographs of both species here discussed and a redescription of *A. alcestis* are given. Although the anatomies of its included species are unknown, the genus *Austrodaphnella* is here assigned to the subfamily Raphitominae in accordance with previous workers. The protoconch and teleoconch morphologies of both species here discussed are consistent with such allocation.

Under the cladistic classification of the superfamily Conoidea recently proposed by Taylor, Kantor and Sysoev (1993), the subfamily Daphnellinae (= Raphitominae), previously included in the family Turridae, is transferred to the Conidae. However, this proposed classification has recently been criticized by Rosenberg (1999), who demonstrated that their results cannot be adequately replicated. As a consequence, this paper still follows the traditional arrangement. Abbreviations used in the text are: a/l = ratio of aperture length to total shell length; b/l = ratio of shell breadth to total length; BMNH = The Natural History Museum, London; MZB = Museo di Zoologia dell' Università di Bologna.

SYSTEMATICS

Family Turridae H. and A. Adams, 1853
Subfamily Raphitominae Bellardi, 1875
Genus *Austrodaphnella* Laseron, 1954

Austrodaphnella Laseron, 1954, p. 45, type species: *Austrodaphnella clathrata* Laseron, 1954 by original designation

Diagnosis: Shell thin, very small to small (up to 10 mm in length), fusiform, superficially resembling genus *Daphnella*, but totally lacking fine interstitial axial riblets. Sculpture of axial ribs crossed by few widely spaced spiral ridges forming quadrangular interstices. Anal sinus subsutural and very slight. Protoconch multispiral to paucispiral, diagonally cancellate or with rows of spirally aligned granules.

Range: Red Sea, Gulf of Oman and Australian waters, from 9 to 256 m.

Remarks: Laseron (1954), in his revision of the New South Wales turrid fauna, erected the genus *Austrodaphnella* for a single species, namely *A. clathrata* dredged from off Pittwater. According to its describer, *Austrodaphnella* differs from the genus *Daphnella* Hinds, 1844 in possessing a fusiform shell with a dis-

tinctly produced, instead of ovate, base and a coarsely clathrate sculpture lacking fine interstitial axial riblets. Powell (1966: 124) regarded *Austrodaphnella* as a valid genus included within the Daphnellinae (= Raphitominae), an opinion recently followed by Sysoev (1993).

Shuto (1983) described a second species, namely *Austrodaphnella torresensis*, based on few damaged shells dredged from off Murray Island, Torres Strait, Queensland. Shuto regarded the species as distinctive because of its peripheral angulation and commented (op. cit.: 24): "it is a problem whether it is included in *Austrodaphnella* Laseron, 1954 or it represents a new subgenus or genus". We have not examined the type series of *A. torresensis*, but its morphological features seem not distinctive enough to warrant a supraspecific distinction from *A. clathrata*.

In this paper, we regard the taxon *Austrodaphnella* as a valid genus on the basis of its teleoconch sculpture, which differs considerably from that of *Daphnella* Hinds, 1844, this latter being a widely distributed genus well represented in the tropics.

Species assigned to *Daphnella* bear dense and minute axial riblets crossed by spiral lirae. In some species the spiral lirae are numerous and nearly equally thin as the riblets forming a very fine reticulation (e.g., *Daphnella botanica* Hedley, 1918), but lirae may also be much fewer and stronger than axial elements (e.g., *Daphnella subula* (Reeve, 1845)), rendering a distinctly carinate aspect to the teleoconch whorls (e.g., *Daphnella sabrina* Melvill, 1906). Some other *Daphnella* species have distinct axial ribs on early teleoconch whorls, but this ornamentation becomes completely obsolete on the last whorl, where the axial sculpture is represented only by rather thin riblets that produce, at most, a slight beading at the intersections with the spiral lirae.

The genus *Austrodaphnella* has widely spaced axial ribs crossed by few spiral ridges, forming relatively broad, quadrangular interstices. The axial sculpture is well developed on all teleoconch whorls, and the minute riblets observed in *Daphnella* are totally lacking. In addition to the difference in sculpture, species assigned to *Austrodaphnella* have a well-produced and strongly excavated base rendering the last whorl conspicuosly more inflated than the penultimate one. This feature, in addition to the thin shell, the relatively few teleoconch whorls, and the very shallow anal sinus, may give the shell a somewhat juvenile appearance. This presumably led Laseron (1954), in his description of *Austrodaphnella clathrata*, to observe that "the type may not be quite mature". Melvill (1906: 78), probably due to the small size and the general appearance of the shell, also considered the described specimen of his *Daphnella* (*Pleurotomella*) *alcestis*, a species here assigned to *Austrodaphnella*, as probably immature. However, referring to other specimens of the species, he noted that "the six or eight examples that occurred were all much of the same size". The somewhat immature appearance noted for the two above-mentioned species is also present in *A. yemenensis*. Although determination of the adult state may be somewhat problematic in species lacking a terminal varix or swelling, it seems unlikely that all these species are actually based solely on juvenile specimens.

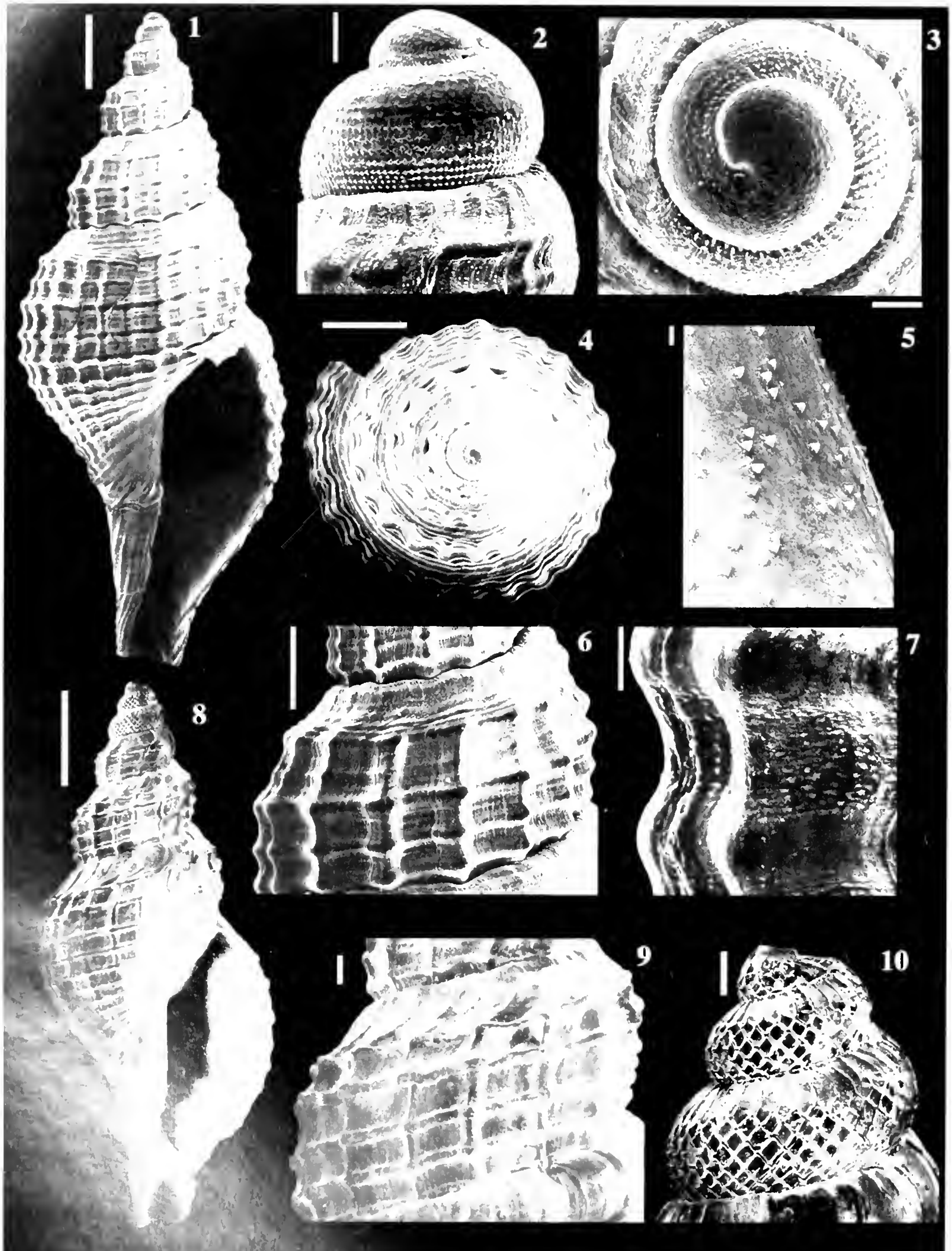
The genus *Daphnella* differs distinctly in this respect from *Austrodaphnella* in possessing a less produced and usually more shallowly excavated base, which gives the last whorl a more elongate-ovate shape. Furthermore, in many *Daphnella* species the anal sinus, though not necessarily deep, is nevertheless distinct; the species assigned to *Austrodaphnella*, as stated above, have a nearly imperceptible sinus. Whether these differences between the two taxa are of generic or subgeneric rank is a matter of opinion. However, the genus *Daphnella*, as presently construed, seems to represent an overcrowded and heterogeneous assessment of species ranging from the Eocene to Recent. Possibly, anatomical studies on some of these species might produce evidence allowing separation of *Daphnella* into different genera or subgenera. Examples of similar situations in other turrid groups are taxa such as *Crassispira* Swainson, 1840, and *Eucithara* Fischer, 1883, belonging respectively to the subfamilies Crassispirinae and the Mangeliinae. Both these two genera are currently accepted as composed by several different groups recognized on the basis of the shell morphology and/or radular features (see for example McLean, 1971; Kilburn, 1992). The taxon *Austrodaphnella* seems to represent a small but distinctive group of species possessing similar shell proportions and sculpture, and is probably worthy of recognition as a genus separate from *Daphnella*, even if its anatomical features are presently unknown.

Apart from *A. clathrata* Laseron, 1954 and *A. torresensis* Shuto, 1983, both from Australian waters, there are at least two other species from the Arabian Peninsula clearly referable to *Austrodaphnella*. One is hereunder described as *Austrodaphnella yemenensis* new species, the other, *A. alcestis* (Melvill, 1906) new combination, was dredged from off the Gulf of Oman and has never been recorded since.

Austrodaphnella yemenensis new species
(Figures 1–7)

Diagnosis: Shell up to 8.6 mm in length, last whorl with 21–25 axial ribs decussated by 4 main spiral ridges. Subsutural ramp and interstices between ridges with secondary sculpture. Protoconch paucispiral, with granular spiral threads.

Description: Shell with a slightly cyrtoconoid spire teleoconch consisting of 4.2 rapidly expanding whorls with strongly impressed suture. Whorls profile weakly shouldered. Subsutural ramp narrow and weakly concave, sculptured by 6–7 (on last two whorls) very low spiral threads and very fine axial incremental lines. Aperture oblanceolate, gradually tapering to siphonal canal. Siphonal canal moderately wide, lacking a terminal notch. Outer lip rather thin, not preceded by a labial varix and smooth inside. Columella rather long and gent-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ly convex. Parietal region slightly convex. Labial callus a thin glaze. SEM examination shows surface of inner lip covered with microscopic, sparse, somewhat squamiform granules (figure 5). Anal sinus reversed, L-shaped. Stromboid notch absent. Sculpture consisting of narrow, slightly angular axial ribs crossed by widely spaced spiral ridges to form spirally elongate interstices. Axial ribs orthocline, nearly equal in width to intervals or about half their width, obsolete on subsutural ramp, fading on last whorl at level of upper part of columella. There are 18 axial ribs on penultimate whorl, increasing to 21–25 on last whorl. First teleoconch whorl with 3 spiral ridges, subsequent whorl with 3–4 main spiral ridges. The first ridge, at the lower edge of the subsutural ramp, is double-spaced from the remaining ones. On later two teleoconch whorls, an additional weak ridge is observed in the interstice between the first and second ridge. Interstices between spiral ridges with 3–5 (on last two whorls) very low spiral threads. Interstices between spiral threads with a microscopic sculpture of spirally aligned granules (figure 7). Base with 14–15 ridges, those on rostrum long and nearly vertical; interstices between ridges with 1–2 very low threads on posterior part of base, anterior part devoid of secondary elements. Background color from light yellow to tan, with irregular orange blotches on last two whorls. Protoconch papilliform consisting of 1.8 whorls with impressed suture, sculptured by minute spiral threads crossed by finer axial threads to form rows of spirally aligned, minute granules (approximately 16 on last whorl of the holotype). Protoconch diameter 0.41–0.43 mm.

Measurements (in mm): Holotype: Length 8.6, width 3.3, aperture 4.5, b/l 0.38, a/l 0.52; paratype 1: length 8.5, width 3.7, aperture 4.6, b/l 0.43, a/l 0.54.

Type material: Holotype, MZB 17001; Paratype 1, MZB 17002; Paratypes 2–3 MZB 17003. Paratypes 2–3 are fragments lacking the body whorl.

Type locality: Off Yemen, southern Red Sea, 14°46′72″ N, 42°32′82″ E, 76 m depth on muddy sand.

Etymology: The specific name refers to the country where the new species was dredged.

Remarks: This new species is assigned to genus *Austrodaphnella* Laseron, 1954, on the basis of its teleoconch features. *Austrodaphnella yemenensis* is readily separable from its congeners by its short, papilliform protoconch with rows of spirally aligned granules instead of conical and with the typical diagonally cancellate sculpture. The protoconch morphology of the new species may resemble that of the widely distributed Indo-Pacific genus *Eucyclotoma* Boettger, 1895. However members of the latter genus differ from species of *Austrodaphnella* in possessing strong spiral keels on the teleoconch whorls. Furthermore, species assigned to *Eucyclotoma* have a truncated anterior end, a distinct though not exceedingly deep anal sinus, and dense axial interstitial riblets closely resembling in this character species assigned to genus *Daphnella*.

Apart from the protoconch, *A. yemenensis* differs from *A. clathrata* Laseron, 1954, which is of comparable size being only slightly larger (10 × 4.5 mm according to Laseron, 1954) and has similar general shell proportions, in having three rather than two spiral ridges on early whorls and, judging from the original figure (op. cit.: 45, fig. 228) less beaded spiral ridges.

Austrodaphnella alcestis (Melvill, 1906) new combination
(Figures 8–10)

Daphnella (Pleurotomella) alcestis Melvill, 1906: 78, pl. 8, fig. 23

Pleurotomella alcestis Melvill, 1917: 196

Diagnosis: Shell of 5.4 mm in length, last whorl with 27 axial ribs decussated by 5 spiral ridges. Subsutural ramp with arched wrinkles, interstices between spiral ridges lacking secondary sculpture. Protoconch multispiral, diagonally cancellate.

Description (BMNH specimen): Shell with slightly cyrtoconoid spire, teleoconch consisting of about 3 rapidly expanding whorls with impressed suture. Whorls convex, weakly shouldered. Subsutural ramp narrow and weakly concave. Aperture oblanceolate gradually tapering to siphonal canal. Siphonal canal moderately wide, lacking terminal notch. Outer lip very thin, not preceded by labial varix and smooth within. Columella rather long and evenly convex. Parietal region convex. Labial callus a thin glaze. Anal sinus very shallow and broadly U-shaped. Stromboid notch absent. Sculpture consisting of narrow, slightly angular axial ribs crossed by wide-set, spiral ridges to form distinctly quadrangular interstices. Axials orthocline much narrower than intervals between them, forming strongly arched wrinkles on subsutural ramp, evanescing on last whorl at the adapical part of columella. There are 17 axial ribs on penultimate whorl, this number increases to 27 on last whorl. First teleoconch whorl with 4 spiral ridges, the first and weaker just below subsutural ramp. Penultimate whorl with 4

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Figures 1–10. Species of *Austrodaphnella*. **1–7.** Holotype of *Austrodaphnella yemenensis* new species, MZB 17001. **1.** Apertural view. Scale bar = 1 mm. **2–3.** Protoconch, scale bar 100 µm. **4.** Apical view. Scale bar = 1 mm. **5.** Squamiform granules of the inner lip. Scale bar = 10 µm. **6.** Teleoconch whorl. Scale bar = 500 µm. **7.** Microsculpture of teleoconch. Scale bar = 50 µm. **8–10.** Lectotype of *Austrodaphnella alcestis* (Melvill, 1906) new combination. **8.** Lectotype of *Daphnella (Pleurotomella) alcestis* Melvill, 1906, BMNH 1906.10.23.28–9. Scale bar = 1 mm. **9.** Teleoconch. Scale bar = 100 µm. **10.** Protoconch. Scale bar = 100 µm.

ridges and a fine thread at abapical suture. Last whorl with 5 spiral ridges. Base of last whorl with about 16 ridges (those on rostrum nearly faded). Color dull white. Protoconch conical, 0.67 mm diameter, with more than 3 whorls (tip missing) and diagonally cancellate sculpture.

Measurements (in mm): Length 5.4, width 2.3, aperture 3.0, b/l 0.43, a/l 0.56.

Type locality: Gulf of Oman, 24°58′ N, 56°54′ E, 285 m.

Material examined: Two specimens labelled as syntypes stored in BMNH (reg. no. 1906.10.23.28–9). Of these, one agrees with the original description, the other is very different, possibly a specimen of *Clathurella amphiblestrum* Melvill, 1904. The specimen of *Daphnella* (*Pleurotomella*) *alcestis* is here selected as lectotype. The SEM micrographs were taken with the specimen uncoated.

Remarks: This species was originally introduced as *Daphnella* (*Pleurotomella*) *alcestis* Melvill 1906, and compared with *Daphnella lucasi* Melvill, 1904, and *Clathurella amphiblestrum* Melvill, 1904, both from the Gulf of Oman. However, neither of these taxa is actually closely related to the species here discussed, which seems properly assigned to the genus *Austrodaphnella*. *Austrodaphnella alcestis* is readily distinguishable from *A. yemenensis* by its typical diagonally cancellate protoconch sculpture instead of rows of spirally aligned granules. Furthermore, *Austrodaphnella alcestis* (Melvill, 1906) is much smaller (5.4 mm vs. 8.6 mm in length), and lacks the secondary sculpture of spiral threads in the interstices between main ridges. In addition, *A. alcestis* has a dull white shell lacking the orange blotches observed in all the available specimens of *A. yemenensis*. It is comparable with *A. torresensis* Shuto, 1983 in dimensions but differs distinctly from the latter in its convex whorls lacking the peripheral angulation of the Australian species. *Austrodaphnella clathrata* is much larger than *A. alcestis* (10 × 4.5 mm vs 5.4 × 2.3 mm) and has two instead of four spiral ridges on early teleoconch whorls.

Biogeographic remarks: The presence of a genus originally described from the Southern Hemisphere in the Arabian Region may probably be explained considering the effect of the Arabian Sea upwelling. During summer the coastlines of Yemen and Oman are affected by the strong Southwest Monsoon, which blows warm surface water offshore causing its replacement by deep, colder oceanic water. Sheppard et al. (1992) discussed some of the more significant consequences that derive from this event. Among other effects, strong upwelling in tropical regions inhibits coral reef growth and induces the development of macroalgal communities of a temperate rather than tropical nature. Thus, the occurrence in the Arabian Sea of species of *Ecklonia*, a kelp genus otherwise found only in the southern hemisphere (Australia, New Zealand and South Africa), is recognized as probably resulting from the lower water temperatures and nutrient input associated with upwelling. The authors also suggested the possibility that the cold upwelling water, by inhibiting reef growth, may act as an ecological barrier restricting the recruitment of many tropical groups in the Red Sea and the Persian Gulf. It seems possible that larvae of species of *Austrodaphnella* may have found in the Arabian Peninsula environmental conditions favorable to metamorphosis. Sheppard et al. (1992) also noted that the upwelling effects may also be strong along the Somali coastline. A possible example supporting this view is the occurrence off Mogadiscio of *Pseudexomilus fuscoapicatus* Morassi, 1997, a species belonging to a genus known otherwise only from South Africa, southern, and eastern Australia.

Austrodaphnella yemenensis differs from all others species assigned to the genus *Austrodaphnella* in protoconch morphology (paucispiral instead of multispiral). This difference is generally regarded as indicative of two different types of developmental strategies, i. e., nonplanktotrophic *versus* planktotrophic development. However, it is generally agreed that different types of larval dispersal may develop in species of the same genus, so that a species with a paucispiral protoconch does not necessitate inclusion in a genus separate from that including species with multispiral protoconchs (Bouchet, 1990).

A number of environmental factors associated both to geographic and climatic factors (such for example geographic isolations, temperature changes, eustatic, and salinity changes), may act in promoting loss of planktotrophy. Planktotrophic species have a prolonged larval life and are therefore more exposed to physical and biological factors increasing larval mortality rates (Rumrill, 1990). Acquisition of lecithotrophic or "direct" larval development may therefore be an ecological adaptation favorably selected in relatively hostile environments characterized by climatic fluctuations (Oliverio, 1996). The dramatic climatic changes in the Arabian Peninsula that particularly affected the Red Sea and the Gulf of Aden during the Quaternary, and the continued strong seasonal temperature fluctuations related to upwelling conditions are factors that probably induced, and may still be inducing, non-planktotrophic larval development.

ACKNOWLEDGMENTS

We wish to thank Dr. Marco Taviani (C.N.R.—Italian National Research Council) Italian partner of European Community project RED SED '92 and Ms. Kathie Way (BMNH) for the loan of type specimens.

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A cladistic analysis of species of *Lambis* (Gastropoda: Strombidae)

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ABSTRACT

A cladistic analysis of the 9 species currently classified as the genus *Lambis* (Abbott, 1961) was conducted. Three species in the genus *Strombus* (Abbott, 1960) were used as outgroups. Features of the radula, soft anatomy, and shell were coded as binary character states (i.e., in a manner that allotted one character state for every bit of information). Each of two most-parsimonious cladograms obtained contains a clade that included all 9 species of *Lambis*, one including a single species of *Strombus* and the other including two. On the basis of this cladistic analysis, *Lambis* is paraphyletic and *Strombus* is polyphyletic. Therefore, the traditional classifications of species within these genera are untenable. The results obtained are used to reassess hypotheses of morphological evolution and adaptive function of circum-apertural projections of strombid gastropods.

Additional key words: Adaptive function, gastropod, information, morphological evolution, phylogenetic systematic analysis.

INTRODUCTION

Lambis (Abbott, 1961) is a genus of marine gastropods endemic to the Indo-Pacific region and a member of the family Strombidae Rafinesque, 1815, which also includes the genus *Strombus* Linnaeus, 1758. Abbott (1961) divided the 9 species currently comprising the genus *Lambis* into three subgenera: *L. lambis* (Linné, 1758), *L. crocata* (Link, 1807), and *L. truncata* (Humphrey, 1786) comprise the subgenus *Lambis* s.s. Röding, 1798; *L. millepeda* (Linné, 1758), *L. digitata* (Perry, 1811), *L. robusta* (Swainson, 1821), *L. scorpius* (Linné, 1758), and *L. violacea* (Swainson, 1821) comprise the subgenus *Millepes* Mörch, 1852; and *L. chiragra* (Linné, 1758) is the lone member of the subgenus *Harpago* Mörch, 1852.

The most outstanding morphological feature of species of *Lambis* is the set of "circum-apertural projections" emanating from the edge of the flared apertural lip of the shell. The number of circum-apertural projections (excluding the siphonal canal) varies among species, ranging from 5 (e.g., *L. chiragra*) to 11 (e.g., *L. violacea*) excluding 7. Circum-apertural projections have been shown to confer protection against crushing (Palmer, 1979), postulated to have evolved as a response to predation (Vermeij, 1989), and hypothesized to provide stability on substrates (via "snowshoeing," or weight distribution) and a means of circumventing geometric constraints during ontogeny (Savazzi, 1991). Circum-apertural projections also might enhance stability via hydrodynamic processes (i.e., drag forces might counteract lift forces produced by currents or waves). Any combination of these factors might be responsible, through evolution, for the existence of circum-apertural projections. However, without reference to a rigorous cladistic analysis from which a hypothesis of the evolution of species of *Lambis* can be formulated, explanations of the origin and utility of circum-apertural projections predominantly are speculative.

In this paper, a cladistic analysis of species of *Lambis* is presented. The results obtained were used to reassess hypotheses of morphological evolution and adaptive function of circum-apertural projections.

MATERIALS AND METHODS

Sample material: Information was obtained from examination (e.g., scanning electron microscopy, dissection, observation) of specimens (table 1) and literature (Abbott, 1960, 1961) concerning all 9 species in the genus *Lambis* and three in *Strombus* (*S. bulla* (Röding, 1798), *S. dilatatus* Swainson, 1821, and *S. vomer* (Röding, 1798)).

Statement of characters and definitions of character states: Information was coded into character states representing 63 characters: 19 concerning the radula, 7 concerning the soft anatomy, and 37 concerning the shell (see below and appendix).

Table 1. Species of the family Strombidae examined, museum catalogue identification, collection localities and sample sizes (n). As a consequence of rarity of some of the species involved, only subsamples of specimens were handled directly to extract information for some characters (e.g., to obtain information concerning the radula of *Lambis lambis*, only a single specimen of the two comprising AMSG C306373 were subjected to scanning electron micrography); other specimens and literature were examined to obtain information for other characters.

Taxon	Depository number	Collection locality	n
Strombus dilatatus Swainson 1821	AMSG C306377	Australia	3
Strombus bulla (Röding, 1798)	AMSG C306402	Philippines	1
Strombus vomer (Röding, 1798)	AMSG C306398	Coral Sea	2
Lambis lambis (Linné, 1758)	AMSG C306373	New Guinea	2
	ANSP[d] 246931	Philippines	2[p]
	ROM Acc 1990-039	NLI	2
Lambis truncata (Humphrey, 1786)	AMSG C306406	Coral Sea	1
	ANSP 237062	New Caledonia	2
	ANSP[d] 215318	Marianas	1[p]
	ROM Acc 1989-051	Oman Muscat	1
Lambis crocata (Link, 1807)	ANSP[d] 212819	Zanzibar	2[p]
	ROM Acc 1987-043	Philippines	4
Lambis millepeda (Linné, 1758)	AMSG C306371	Philippines	1
	ANSP[d] 228924	Philippines	8[p]
	ROM Acc 199-039	NLI	1
Lambis digitata (Perry, 1811)	ROM 1995-001	Tanzania	1
Lambis robusta (Swainson, 1821)	AMSG C306375	Society Islands	1
Lambis scorpius (Linné, 1758)	AMSG C306374	New Guinea	1
	ANSP 206391	New Guinea	1
	ANSP[d] 39879	Zanzibar	1[p]
	AMSG 306374	New Guinea	1
Lambis chiragra (Linné, 1758)	AMSG C306372	Australia	1
	ANSP 212429	Zanzibar	3
	ANSP[d] 201470	Palau Islands	1[p]
	ANSP 223975	Philippines	1
	ROM Acc 1987-055	Indo-Pacific	1

[d] = dry specimens (i.e. shell only)
[p] = photographic plate of specimen included in Abbott 1960 or Abbott 1961

Radula

Strombid species possess a taenoglossate radula consisting of rows of seven teeth (figure 1): a central (median, or 'rachidian') tooth flanked on either side by a single lateral tooth and two marginal teeth (or 'uncini').

Characters 1–4: *Type of tooth cusps.* Absence (0) or presence (1) of 4 types of tooth cusps were defined and coded as binary character states: obtuse-tipped, apiculate-tipped, 'millepedoid,' and 'chiragroid' (figures 2–5).

Characters 5–6: *Number of cusps flanking central teeth.* Central teeth possess a single medial cusp flanked on either side by smaller cusps in a series (figures 6–7). Absence (0) or presence (1) of 2 and 3 cusps in the series were defined and coded as binary character states.

Characters 7–10: *Number of cusps of lateral teeth.* Most strombid species possess lateral teeth with a single large cusp adjacent to the central tooth and smaller cusps in a series that extends toward the inner marginal teeth. Absence (0) or presence (1) of 2, 3, and 4 cusps in the series were defined and coded as binary character states. One species, *S. dilatatus*, has lateral teeth with 4 equivalent cusps; this condition also was coded as a binary character state.

Characters 11–14: *Number of cusps of inner marginal teeth.* Absence (0) or presence (1) of specific numbers of cusps of inner marginal teeth were defined and coded as binary character states: 1, 5, 6, and 7.

Characters 15–19: *Number of cusps of outer marginal teeth.* Absence (0) or presence (1) of specific numbers of cusps of outer marginal teeth were defined and coded as binary character states: 1, 5, 6, 7, and 8.

Soft parts

Characters 20–21: *Type of mouth.* Some strombid species burrow into substrata, using their acrembolic snouts to displace sediment (Savazzi, 1991). Absence (0) or presence (1) of a 'stromboid' and an elongate mouth (figures 8–9) were defined and coded as binary character states.

Characters 22–26: *Number of serrations of the operculum.* Strombid species possess a sickle-shaped operculum that fills the aperture incompletely. As most strombids do, species of *Lambis* use the operculum as a lever during 'vaulting,' or leaping locomotion (Savazzi, 1991). Occasionally, such behavior results in overturning; righting is accomplished by lifting the operculum over

Figure 1. Scanning electron micrograph of taenoglossate radula typical of species of Strombidae (*Lambis millepeda*; bar = 150 μm).

the left side of the animal, lowering the operculum into the substratum, and kicking laterally (Savazzi, 1991). A similar opercular motion has been observed as a defense mechanism against fish and crab predators (Jung and Abbott, 1967; Melvin, 1973; Savazzi, 1991; Vermeij, pers. comm.). The operculum is smooth (i.e. has 0 serrations) or denticulated with 7, 8, 10, or 16 serrations. Absence (0) or presence (1) of specific numbers of serrations of the operculum were coded as binary character states.

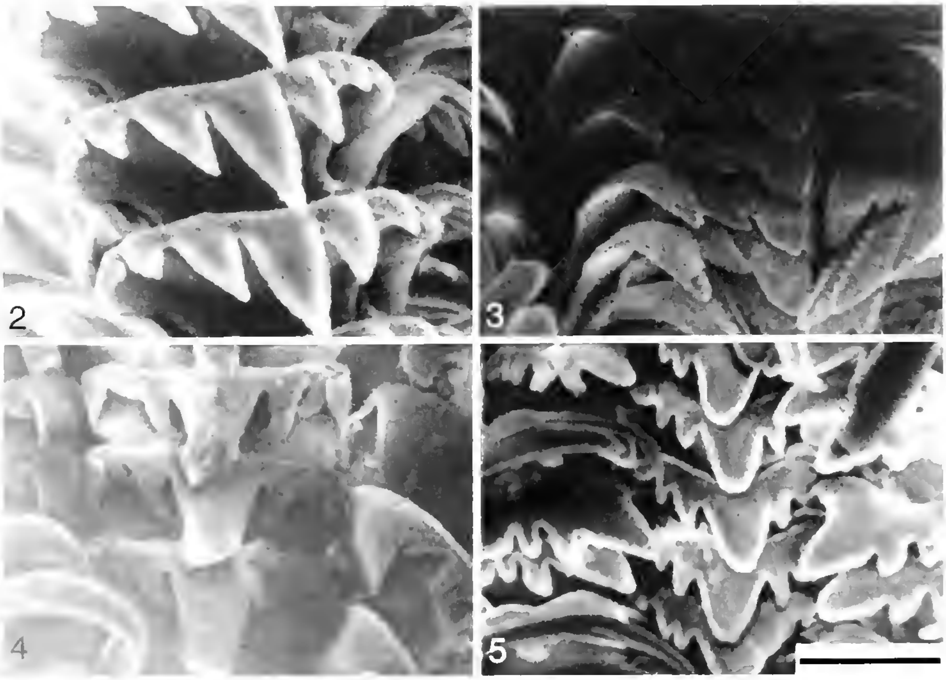
SHELL

Characters 27–29: *Number of whorls.* Absence (0) or presence (1) of 9, 10, and 11 whorls were defined and coded as binary character states.

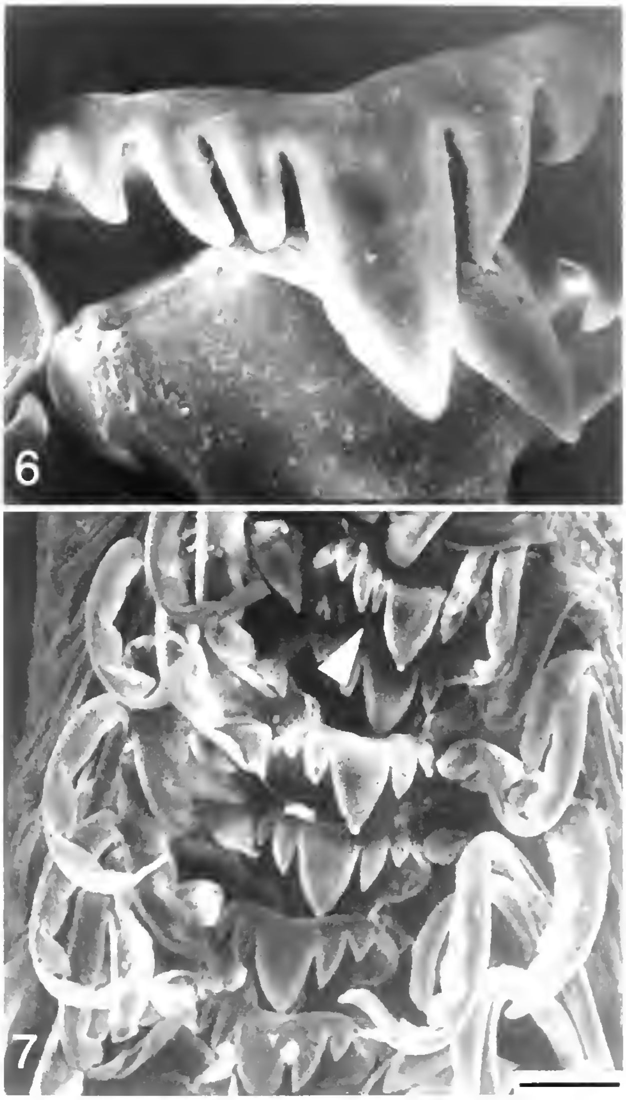
Character 30: *Form of protoconch.* The protoconch of the shell of some strombid species is sculptured. Possession of an unsculptured (0) or a sculptured (1) protoconch were defined and coded as distinct character states.

Characters 31–35: *Type of sculpture of whorls.* The whorls of the shell of strombid species exhibit a variety of sculptures. Absence (0) or presence (1) of 5 types of sculpture of whorls were defined and coded as binary character states: cords, lines, ribs (longitudinal, narrow ridges; Arnold, 1965), threads (slender surface elevations; Arnold, 1965), and beads.

Characters 36–38: *Type of sculpture of columella.* The columella of strombid species exhibits a variety



Figures 2–5. Types of cusps of radular teeth of some species of Strombidae (characters 1–8). **2.** Apiculate-tipped (*Strombus haemastoma* Sowerby, 1842; bar = 50 μm). **3.** Obtuse-tipped (*Lambis truncata*; bar = 650 μm). **4.** 'Millepedoid' (*L. millepeda*; bar = 150 μm). **5.** 'Chiragroid' (*L. chiragra*, bar = 150 μm). Differences among types were determined on the basis of form.

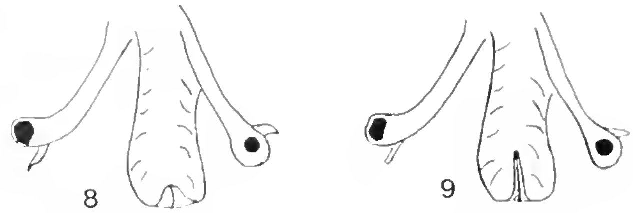


Figures 6, 7. Number of cusps flanking central teeth of some species of Strombidae (characters 9–12). **6.** Central tooth of a specimen of *Strombus variabilis* Swainson, 1820 with 2 or 3 flanking cusps (bar = 25 µm). **7.** Central tooth of *Strombus marginatus* Linné, 1758 with 2 or 3 flanking cusps (one of the three cusps is indicated with a white wedge; bar = 75 µm).

of sculptures. Absence (0) or presence (1) of a smooth surface, lirae (fine, parallel grooves; Arnold, 1965), and ribs were defined and coded as binary character states.

Characters 39–45: *Color of columella.* The columella of the shell of strombid species exhibits a variety of colors. Absence (0) or presence (1) of 7 colors were defined and coded as binary character states: white, black, orange, brown, purple, pink, and mauve.

Characters 46–54: *Color of aperture.* The aperture of the shell of strombid species exhibits a variety of colors. Absence (0) or presence (1) of 9 colors were defined and coded as binary character states: white, yellow, purple, brown, rose, tan, mauve, cream, and orange.



Figures 8–9. Types of mouth of some species of Strombidae (characters 39–42). **8.** stromboid. **9.** 'elongate'.

Character 55: *Torque of siphonal canal.* The siphonal canal of the shell of some strombid species is twisted about its own axis. Possession of an untwisted (0) or a twisted (1) siphonal canal were defined and coded as distinct character states.

Character 56: *Curvature of siphonal canal.* The siphonal canal of the shell of some strombid species is curved in the plane of the aperture. Possession of a noncurved (0) or a curved (1) siphonal canal were defined and coded as distinct character states.

Characters 57–63: *Number of circum-apertural projections.* Shells of lambid species provide some of the most striking examples of sexual dimorphism among marine gastropods. Shells of females are larger than are those of males, and, in addition, there are differences of shape. For example, circum-apertural projections emanating from shells of female *Lambis lambis* are directed dorsally, whereas those of male *L. lambis* are directed posteriorly. During copulation, each participant positions its shell so that its stromboid notch (a parabolic impression at the anterior portion of the aperture of the shell of most strombid species) is adjacent to that of its partner. This spatial arrangement of circum-apertural projections enhances close positioning of shells and may facilitate coition (Abbott, 1961). Absence (0) or presence (1) of specific numbers of circum-apertural projections were defined and coded as binary character states: 1, 5, 6, 8, 9, 10, and 11.

Cladistic Analysis: Cladistic analysis of the data (see above and appendix) was conducted using the computer program Hennig86 (Farris, 1988), designating the three species of *Strombus* as outgroups (as they are co-familial with species of *Lambis*; Abbott, 1960) and invoking the implicit enumeration option **ie** (which determines a maximum of 100 equally most-parsimonious cladograms). Each of the three species of *Strombus* was invoked as the primary outgroup in three separate analyses. Autapomorphic character states were omitted from analyses to avoid inflating consistency indices (Wiley et al., 1991). To provide a measure of node support, the bootstrap resampling procedure was conducted (Sanderson, 1989; Hillis and Bull, 1993; Felsenstein and Kishino, 1993; Sanderson, 1995; Carpenter, 1996) using the computer program Random Cladistics (Siddall, 1997). Clades were obtained by cladistic analysis of the original data matrix; the percent occurrences of partic-

ular clades thus defined in cladograms resulting from cladistic analysis of data matrices created by resampling were determined (this procedure differs from that described in Felsenstein, 1985, which yields a "bootstrap estimated phylogeny"). It was assumed that characters were unassociated and character states were independent.

RESULTS AND DISCUSSION

Two most-parsimonious cladograms were obtained (length = 93, consistency index = 45, retention index = 46), one if either *Strombus bulla* or *S. dilatatus* was designated as the prime outgroup and one if *S. vomer* was (figures 10–11). Each of these cladograms contained a clade that included all 9 species of *Lambis*, one including *S. vomer* and the other including *S. bulla* and *S. dilatatus*. Bootstrap values ranged from 0 to 38%.

Cladogram: In a cladistic analysis, character states of each character are considered with respect to character states of each of the other characters, and the cladogram obtained represents the most parsimonious grouping of potentially mutually exclusive hypotheses of clade membership. The structures of the cladograms containing species of *Lambis* were predominantly determined by character states associated with the radula and shell (which comprise 56 of the 63 characters: figures 10–11). In particular, there is a tendency for characters concerning the radula (characters 1–19) to be represented by synapomorphic states that determine the basal structure of the cladograms and for characters concerning the shell (characters 27–63) to be represented by synapomorphic states that determine terminal structure. There is a tendency for characters concerning the soft body to be represented by autapomorphic character states.

One cladogram is completely pectinate (figure 10), whereas the other includes a clade containing species of *Lambis* and *Strombus* (figure 11). Within the completely pectinate cladogram, *S. bulla*, *S. dilatatus*, *L. crocata* (a member of the subgenus *Lambis*), and *S. vomer* sequentially are sister groups of all other taxa. within the incompletely pectinate cladogram, *S. vomer* is the sister group of all other taxa, and *L. crocata* is the sister group of the clade comprised of *S. bulla* and *S. dilatatus* (this clade was determined by the absence of tricuspid lateral teeth (character 8), hexacuspic outer marginal teeth (character 17), beaded whorl sulpture (character 35), and lirae (character 37) and the presence of smooth whorl sculpture (character 36) and a brown colored columella (character 42)).

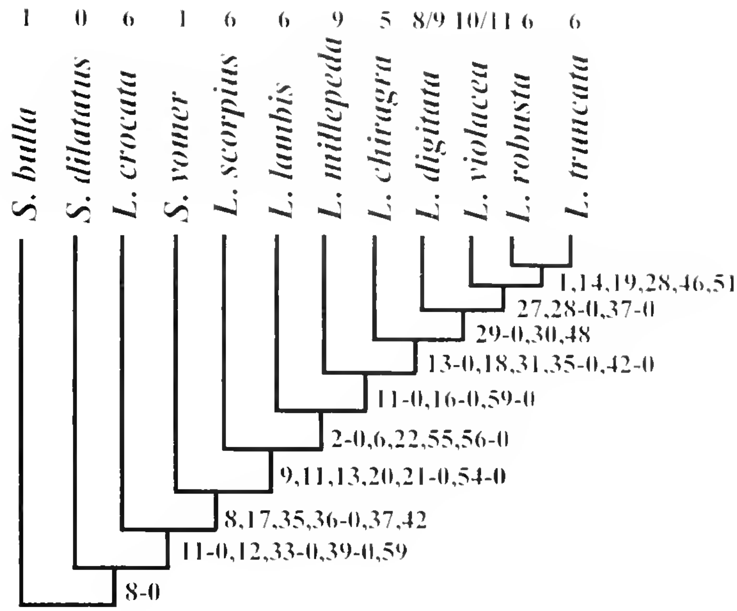
The classifications obtainable from the cladograms (figures 10–11) are inconsistent with previous classifications of the family Strombidae and its member genera (e.g., Abbott, 1960, 1961): *Lambis* is paraphyletic, and *Strombus* is polyphyletic. The classifications also are incompatible with current subgeneric assignments: the subgenus *Lambis* (*L. lambis*, *L. crocata*, and *L. truncata*) is polyphyletic, whereas the subgenus *Millepes* (*L. scorpius*, *L. millepeda*, *L. digitata*, *L. robusta*, and *L. violacea*) is paraphyletic and includes the lone member of the subgenus *Chiragra* (*L. chiragra*). Because previous classifications of strombid species were established noncladistically on the basis of similar information, the incompatibility of these hypotheses with previous classifications results from the previously undocumented variation observed and the hypothetico-deductive testing involved in cladistic analysis.

Since the publication of Abbott's (1961) monograph, two new species of the subgenus *Millepes* have been described solely on the basis of information concerning shells: *Lambis arachnoides* Shikama, 1971 (Shikama, 1971) and *L. wheelwrighti* Greene, 1978 (Greene, 1978). Kronenberg (1993) concluded that both taxa refer to hybrids of *L. truncata sebae* (a member of the subgenus *Lambis*) and *L. millepeda* (the type species of the subgenus *Millepes*), as hybridization between members of their respective subgenera occurs (e.g., *L. scorpius scorpius* × *L. crocata crocata*, and *L. millepeda* × *L. lambis*) and shell morphologies of hybrids are intermediate between those of the two putative parent species.

The subgenus *Millepes* is characterized by ". . . elongate apertures bearing well developed lirae, by a siphonal canal which is either straight or curved to the right, and by the presence of six to ten labial digitations" (Abbott, 1961). Kronenberg (1993) suggested that, because species of the subgenus *Lambis* have elongated apertures, variably shaped siphonal canals, and 6 circum-apertural projections, the presence of lirae might remain as the only diagnostic character state of *Millepes*. However, *L. truncata sebae* can exhibit lirae on the outer lip (Kronenberg, 1993). Given this observation and the fact that hybridization between members of the subgenera *Millepes* and *Lambis* occurs, Kronenberg (1993) suggested that these two taxa should be synonymized and the concept of *Millepes* as a subgenus should be abandoned.

Abbott (1961) offered a cautionary remark concerning systematics of *Lambis*: " . . . from a biological standpoint, some workers might wish to consider them a subgenus of *Strombus*." On the basis of this cautionary remark, Kronenberg's (1993) observations and conclusions, and the cladograms obtained, the validity of current generic and subgeneric classifications of *Strombus* and *Lambis* are dubious and, consequently, the current classification of the family Strombidae is untenable.

Reassessing hypotheses of morphological evolution and function of circum-apertural projections: The cladograms containing species of *Lambis* (figures 10–11) may be used to reassess hypotheses of morphological evolution of circum-apertural projections, by considering distributions of character states representing numbers of circum-apertural projections on terminal nodes as "attributes" (sensu Deleporte, 1993), inferring most-parsimonious character state transformations, and interpreting branching patterns to represent reconstructions of phylogenetic history (because the outgroup criterion for



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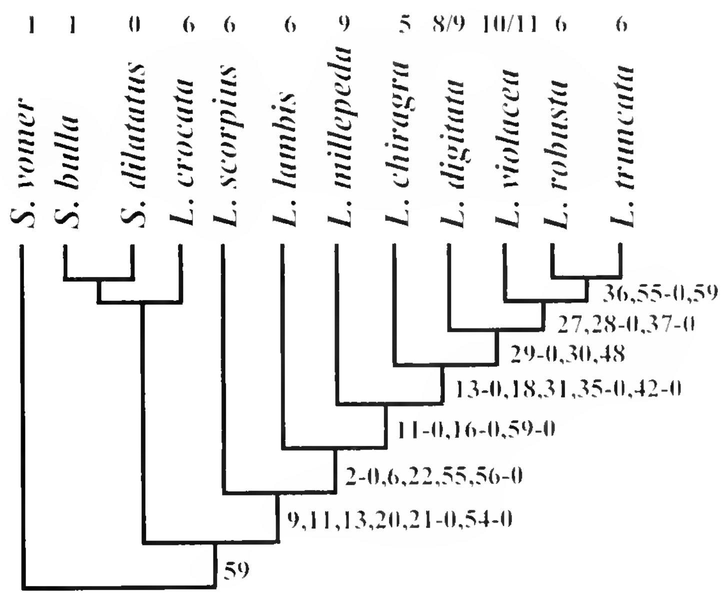

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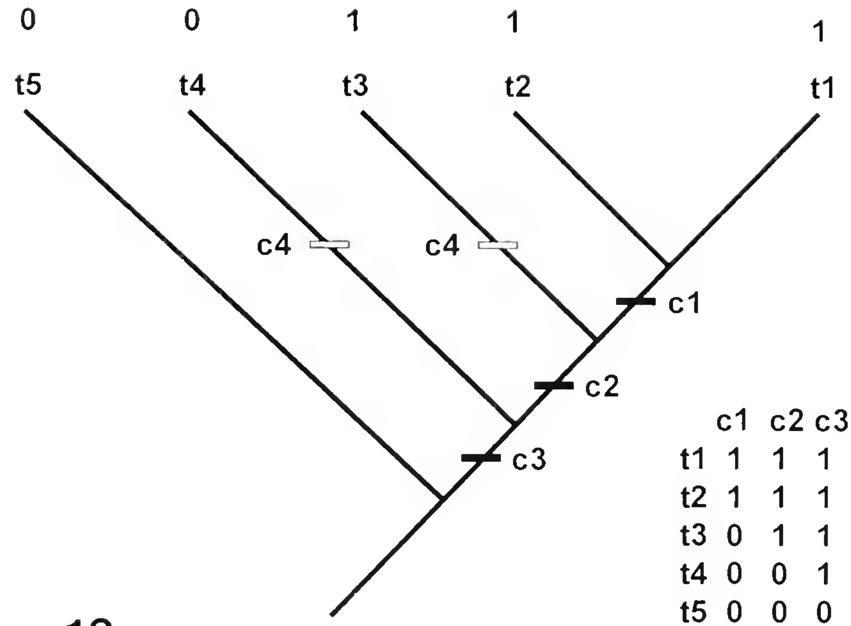
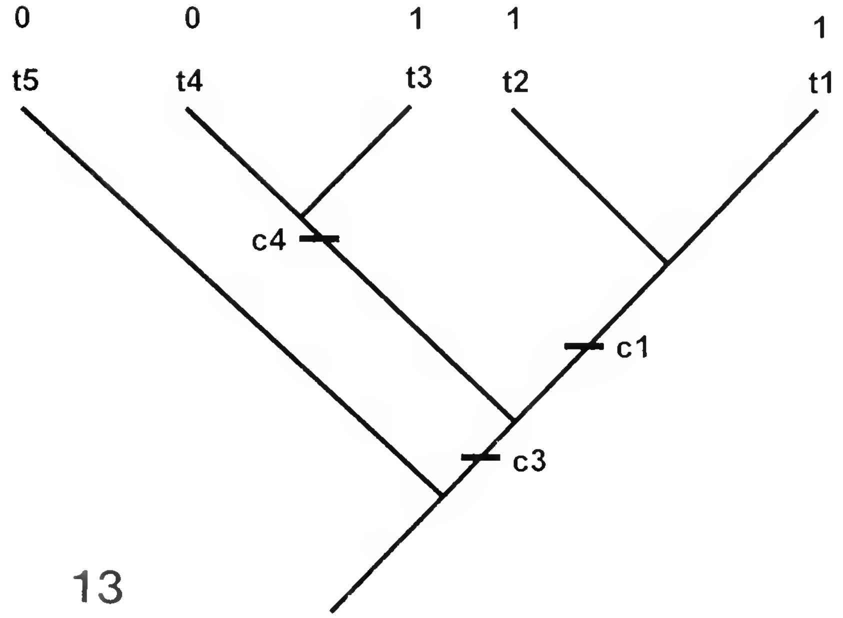
Figures 10–11. Cladograms (resulting from cladistic analysis of data described in Materials and Methods) that include species currently classified as *Lambis* (characters are indicated by numbers, and character states are 1 unless specified with -0). Synapomorphic character states are indicated on internodes, except for those shared by *S. bulla*, *S. dilatatus*, and *L. crocata* (8-0, 17-0, 35–0, 36, 37–0, 42) and those shared by *S. bulla* and *S. dilatatus* (11, 12–0, 24, 33, 59-0). Autapomorphies are omitted for clarity (*S. bulla*: 8, 27, 31, 50, 55, 57; *S. dilatatus*: 10, 16–0, 17, 30, 32, 34-0, 38, 39, 46, 48, 49, 54-0; *S. vomer*: 23, 24, 28-0, 38, 41, 57; *L. crocata*: 7, 22; *L. scorpius*: 12–0, 25, 27, 43, 48; *L. lambis*: 1, 15, 36, 37-0, 40, 50, 51, 53, 54; *L. millepeda*: 3, 8-0, 28-0, 34-0, 44, 52, 61; *L. chiragra*: 4, 22–0, 26, 43, 44, 46, 58; *L. digitata*: 45, 52, 60, 61; *L. violacea*: 62, 63; *L. robusta*: 2, 5–0, 9–0, 11, 42, 48–0, 53, 56; *L. truncata*: 1, 14, 19, 28, 46, 51). Specific numbers of circum-apertural projections are indicated on terminal nodes.



	c1	c2	c3	c4
t1	1	1	1	0
t2	1	1	1	0
t3	0	1	1	1
t4	0	0	1	1
t5	0	0	0	0

12



13

Figures 12–13. [illegible]nstructing evolution of attributes. A cladistic data matrix consisting of the 5 taxa t1–5 and 4 characters c1–4 is used to con[illegible] two cladograms on the terminal nodes of which character states of character 2 are distributed as "attributes" sensu Deleporte [illegible] for historic reconstruction. **12.** The character states of character c2 are included in the cladistic analysis. **13.** The character states of character c2 are excluded. The two cladograms differ, demonstrating that, by excluding attributes from a cladistic analysis, different cladograms could be used to test hypotheses concerning the same group of taxa, using the same characters. Including attributes is the more consistent procedure logically.

character-state coding is independent of evolutionary processes, the coding of each apomorphy is independent of the structure of the entire cladistic data matrix, the cladogram resulting from cladistic analysis, and the phylogenetic interpretation of that cladogram; thus, there is no logical circularity in including attributes as characters in cladistic analyses—i.e., apomorphies are "primary statements," and phylogenetic hypotheses are "secondary statements" (sensu Deleporte, 1993); in fact, by excluding an attribute, different cladograms would be used to test hypotheses concerning the same group of taxa using the same characters (figures 12–13; Deleporte, 1993)). The most-parsimonious hypotheses concerning the number of circum-apertural projections present upon their origin are equivocal: on the basis of the completely pectinate cladogram, the ancestor of all the species possessed a set comprised of either 0, 1, or 6 circum-apertural projections; on the basis of the incompletely pectinate cladogram, the ancestor of all the species possessed a set comprised of either 1 or 6. Subsequent to the origin of this prominent feature, the number of circum-apertural projections was modified independently with the origins of *L. millepeda*, *L. chiragra*, *L. digitata*, and *L. violacea*.

These cladograms also can be used to formulate hypotheses of functions of circum-apertural projections. Circum-apertural projections have been shown to confer protection against crushing (Palmer, 1979), and it has been postulated that they have evolved as a response to predation (Vermeij, 1989). This hypothesis could be tested, by comparing the evolution of circum-apertural projections with the evolution of crushing apparatus of predators, each inferred from independent cladograms. In particular, a correlation should exist between number (and strength conferred by possession) of circum-apertural projections and crushing strength of predators. The hypothesis that circum-apertural projections provide stability on substrates (Savazzi, 1991) could be tested by considering distributions of character states representing numbers of circum-apertural projections and habitats on the terminal nodes of the cladograms and interpreting them phylogenetically. Perhaps a correlation exists between number (and stability provided by possession) of circum-apertural projections and the type of substrate preferred by strombid species, suggesting a remarkable adaptation of form to function or vice-versa. The hypothesis that circum-apertural projections provide means of circumventing geometric constraints during ontogeny (Savazzi, 1991) could be elaborated and tested by integrating information concerning ontogeny into a phylogenetic context. A correlation might exist between numbers of circum-apertural projections and 'time-to-maturation,' which would be discernable by considering distributions of appropriate character states on the terminal nodes of the cladograms. Finally, the possibility that enhanced stability on substrates as a consequence of increased drag conferred by the possession of circum-apertural projections could be tested from within an historical context, by considering biogeographical distributions, tests of fluid-dynamics, and the branching pattern depicted by the cladograms. Correlations among environmental, hydrodynamic, and inferred temporal information would indicate whether numbers of circum-apertural projections have evolved in response to different hydrodynamic environments encountered during evolution. Currently, testing of these hypotheses is delayed by insufficient information concerning predation, lack of knowledge about the evolutionary histories of predators, scant documentation of life-histories, habitats, and development of strombid species, and the paucity of data concerning hydrodynamic properties of their environments.

ACKNOWLEDGMENTS

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Appendix. Data matrix with coding of characters states used in the cladistic analysis of species of *Lambis*. Numbered characters are explained in the text. 0 = absence, 1 = presence, ? = indeterminned.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Strombus bulla	?	?	?	?	1	0	0	1	0	0	1	0	0	0	0	1	0	0	0	?	?	?	?	?	?	?	1	1	1	?	1	0
Strombus dilatatus	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	1	1	1	0	1
Strombus romer	0	1	0	0	1	0	0	1	0	0	0	1	0	0	0	1	1	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0
Lambis lambis	1	0	0	0	1	1	0	1	1	0	1	1	1	0	1	1	1	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0
Lambis truncata	1	0	0	0	1	1	0	1	1	0	0	1	0	1	0	0	1	1	1	?	?	1	0	0	0	0	1	1	0	?	1	0
Lambis crocata	?	?	?	?	1	0	1	0	0	0	0	1	0	0	0	1	0	0	0	?	?	1	0	0	0	0	0	1	1	0	0	0
Lambis millepeda	0	0	1	0	1	1	0	0	1	0	0	1	1	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Lambis digitata	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	?	?	?
Lambis robusta	0	1	0	0	0	1	0	1	0	0	1	1	0	0	0	0	1	1	0	1	0	1	0	0	0	0	1	0	0	1	?	?
Lambis scorpius	0	1	0	0	1	0	0	1	1	0	1	0	1	0	0	1	1	0	0	1	0	0	0	0	1	0	1	1	1	0	?	?
Lambis violacea	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0	?	1	0
Lambis chiragra	0	0	0	1	1	1	0	1	1	0	0	1	0	0	0	0	1	1	0	1	0	0	0	0	0	1	0	1	1	?	1	0

	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
Strombus bulla	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	1	0	0	0	0	0	0
Strombus dilatatus	1	0	0	1	0	1	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Strombus romer	0	1	1	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0
Lambis lambis	0	1	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	1	1	1	0	0	0	1	0	0	0	0
Lambis truncata	0	1	0	1	0	0	?	?	?	?	?	?	?	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0
Lambis crocata	0	1	0	1	0	0	?	?	?	?	?	?	?	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Lambis millepeda	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0
Lambis digitata	?	?	?	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0	0	0	0	1	1	0	0
Lambis robusta	?	?	?	?	?	?	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0
Lambis scorpius	?	?	?	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Lambis violacea	0	1	0	?	?	?	?	?	?	?	?	?	?	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1
Lambis chiragra	0	1	0	0	1	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	?	?	0	1	0	0	0	0	0

Rediscovery of *Canidia dorri* Wattebled, 1886, with discussion of its systematic position (Gastropoda: Neogastropoda: Nassariidae: *Nassodonta*)

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ABSTRACT

Canidia dorri Wattebled, 1886, described from Kao-hai Lagoon (near Hue, Vietnam) but until now known only from its original description, was rediscovered in lower parts of rivers at Phan Ri, central Vietnam. Examination of morphology and radula of the species revealed, that it should be allocated to the family Nassariidae and, according to shell morphology, to the genus *Nassodonta* H. Adams, 1867. This is the first confirmed record of genus *Nassodonta* outside Indian waters. The only other Asian species of the family Nassariidae known to inhabit fresh or brackish waters were found in Lake Chilka and other backwater areas in India.

Additional key words: Gastropod, brackish water, Asia, Vietnam.

INTRODUCTION

During a visit to the Fisheries University in Nha Trang (Central Vietnam), as part of the Tropical Marine Mollusc Program (TMMP), the authors came across a sample of an unusual neogastropod. These specimens possess a deep basal spiral sulcus, similar to that found in the Pseudolividae. They were shown to Dr. Nguyen Ngoc Thach, a mollusk specialist and shell dealer in Nha Trang, who recognized the species and offered to collect additional samples with precise data. A sample was subsequently provided to the authors with the note that the species inhabited the lower parts of Vietnamese rivers. Examination of the radula revealed that the species belongs to the family Nassariidae. It was concluded that the species is congenteric with and closely related to *Nassodonta insignis* H. Adams, 1867.

While examining collections of freshwater neogastropods in Muséum national d'histoire naturelle, Paris, the senior author came across two syntypes of *Canidia dorri* Wattebled, 1886, described from Lagune de Kao-hai, Vietnam. The figured syntype (Wattebled, 1886: pl. III, fig. 5) differed markedly from the second one, which in turn exactly matched our specimens. Fortunately, both syntypes contained a dried body, which allowed us to examine its radulae.

Since *Canidia dorri* seems not to have been reported since its original description, we here give a detailed redescription on the basis of both type material and recently collected specimens.

SYSTEMATICS

Class Gastropoda Cuvier, 1797
Order Neogastropoda Wenz, 1938
Superfamily Buccinoidea Rafinesque, 1815
Family Nassariidae Iredale, 1916
Genus *Nassodonta* H. Adams, 1867

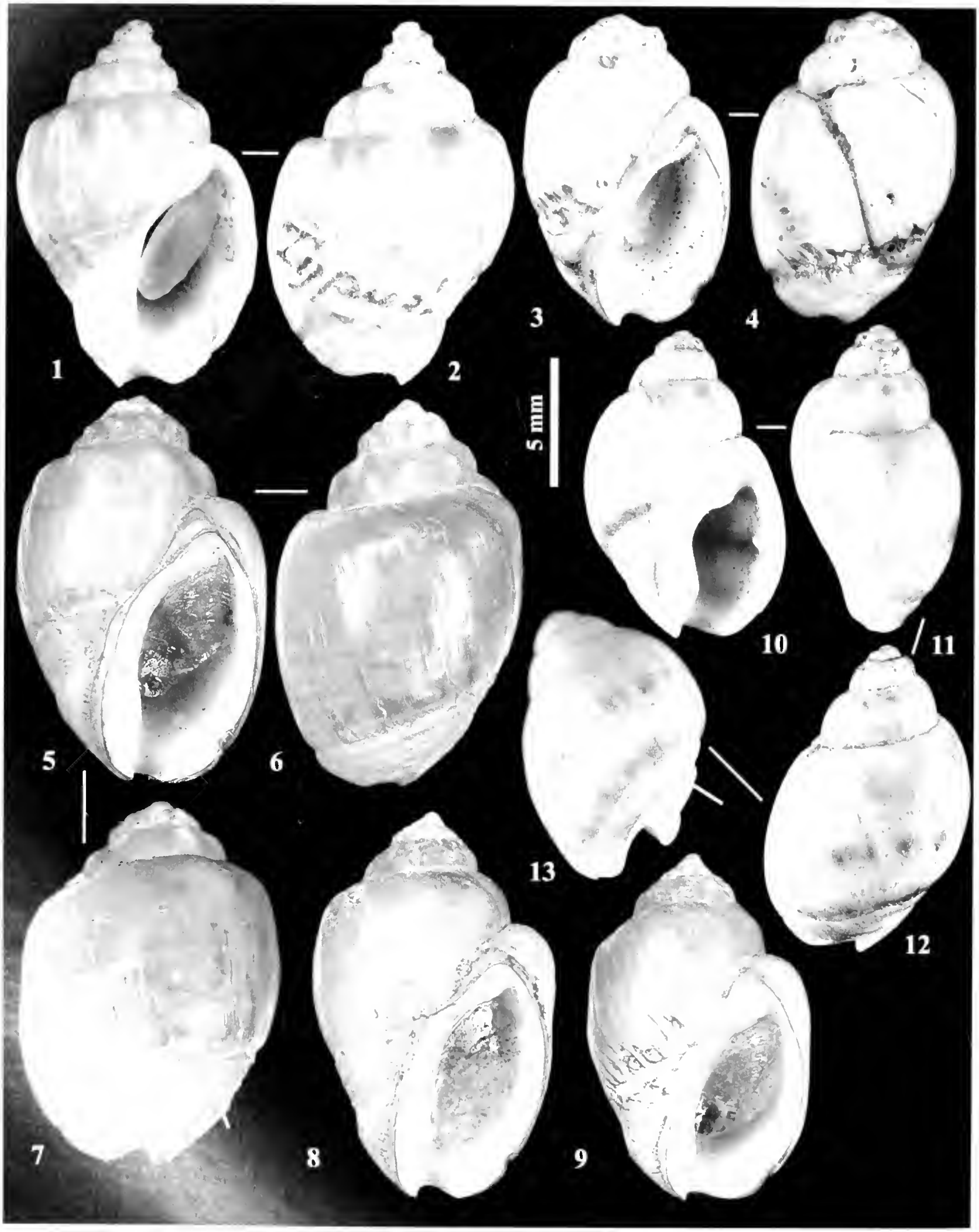
Type species (by monotypy): *Nassodonta insignis* H. Adams, 1867

Remarks: Although Cernohorsky (1984: 199) regarded *Nassodonta* as a subgenus of *Nassarius* Duméril, 1806, we consider it to be a full genus, characterized by the presence of a conspicuously deep basal groove (sulcus) and by its distinctive radula.

The radula of *Nassodonta* (as exemplified by the species here described) resembles that found in the genera *Bullia* and *Buccinanops* (see Cernohorsky, 1984: figs 78–90), rather than typical *Nassarius*, in the prominent development of accessory cusps on the lateral plates and in the less pectinate appearance of the cusps on the rachidian. However, accessory cusps occur in at least one typical *Nassarius* (see Cernohorsky, 1984: fig. 31), and these characters should be regarded as homoplastic.

Although *Nassodonta* was originally described in the Buccinidae, Smith (1895) transferred the genus to the Nassariidae based on shell characters. The presence of a multicuspidate rachidian tooth of the radula, as illustrated here, confirms this family allocation.

The type locality of *Nassodonta insignis* was given as the Peiho River, China (which is possibly the modern



Figures 1–13. Shells of N[illegible] 1–9. N[illegible] *[illegible]tardorii* Wattebled, 1886. **1.** Apertural and **2.** dorsal views of figured syntype MNHN. **3.** Apertural and **4.** [illegible] of syntype MNHN. **5–9.** Specimens from Phan Ri, central Vietnam. **5.** Apertural; **6.**

Hai He River, which enters the sea at Tiensien. However, Smith (1895) pointed out that the actual label accompanying the holotype read "Peihoi" and referred to it as having been collected together with *Velorita* [the corbiculid genus *Villorita* Gray, 1834]. Noting that the latter was an Indian genus and that undoubted examples of *N. insignis* had been collected in India, Smith queried the Chinese origin of the holotype. Preston (1916) and Cernohorsky (1984) confirmed the occurrence of *N. insignis* in India, living sympatrically with a second taxon, *Nassodonta gravelyi* Preston, 1916, which Cernohorsky synonymised with *N. insignis*. It may be noted that the present material from Vietnam greatly extends the overall known distribution of *Nassodonta*, as previously defined by Cernohorsky.

Nassodonta dorri (Wattebled, 1886) new combination
Figures 1–8, 13–16

Canidia dorri Wattebled, 1886: 56–57, pl. IV, fig. 2

Type material: Two syntypes, Muséum national d'histoire Naturelle (figures 1–4).

Type locality: Lagune de Kao-hai (near Hue).

Material examined: Syntypes, 20 specimens from rivers at Phan Ri, now stored at: Zoological Museum of Moscow State University, ZMMU No. Le-25171, 25172; Natal Museum L5452, The Natural History Museum, London, BMNH 20000391; Muséum national d'histoire naturelle, Paris, MNHN unnumbered; National Museum of Natural History, Washington, DC, USNM 905326, 905327; Academy of Natural Sciences, Philadelphia ANSP 403196; Australian Museum C.386612; National Science Museum, Tokyo, NSMT Mo 72688; Zoological Institution, St. Petersburg, ZIN 59584; University of Fisheries, Nha Trang, Vietnam.

Distribution (Figure 21): Central Vietnam, from Hue to rivers at Phan Ri (about 150 km south of Nha Trang). Additional material was collected in the lower parts of rivers, at a depth of about 3 meters.

Description: Shell thick, oblong-ovate, usually with subcylindrical body whorl (broadly fusiform in figured syntype) and low, obtuse spire; whorls distinctly shouldered, spire somewhat cyrtoconoid, apex mamillate. Protoconch eroded in all specimens.

Aperture oblong, lanceolate, constricted anteriorly. Inner lip with wide smooth callus, its outer edge slightly but distinctly raised, without parietal nodule. Outer lip smooth internally, notched in anterior portion, where it is cut by basal sulcus; outer lip strongly thickened behind

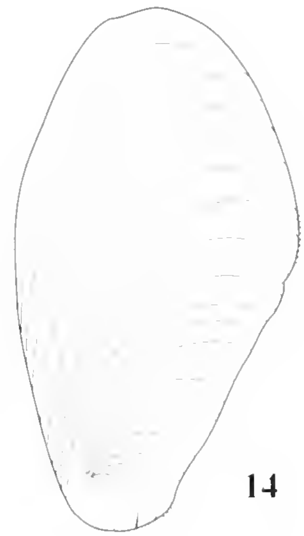


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Figure 14. Operculum of specimen in figs. 5–7, length 5.7 mm.

edge, but not forming varix. Siphonal canal short, moderately narrow, dorsally forming a fairly shallow notch.

Shell surface slightly glossy, spire whorls with strong prosocline axial ribs, in transverse section rounded and wider than intervals. Axial ribs 9–10 on first and second whorl, on spire extending from suture to suture but on later whorls developing into nodules, which become obsolete mid-dorsally. In figured syntype axial ribs are present on the last whorl, there totalling 10.

Base of last whorl at level of parietal columellar junction with a deep, asymmetrically cut furrow. Fasciole convex with growth lines only. Area between fasciole and basal groove with 1–3 spiral ridges.

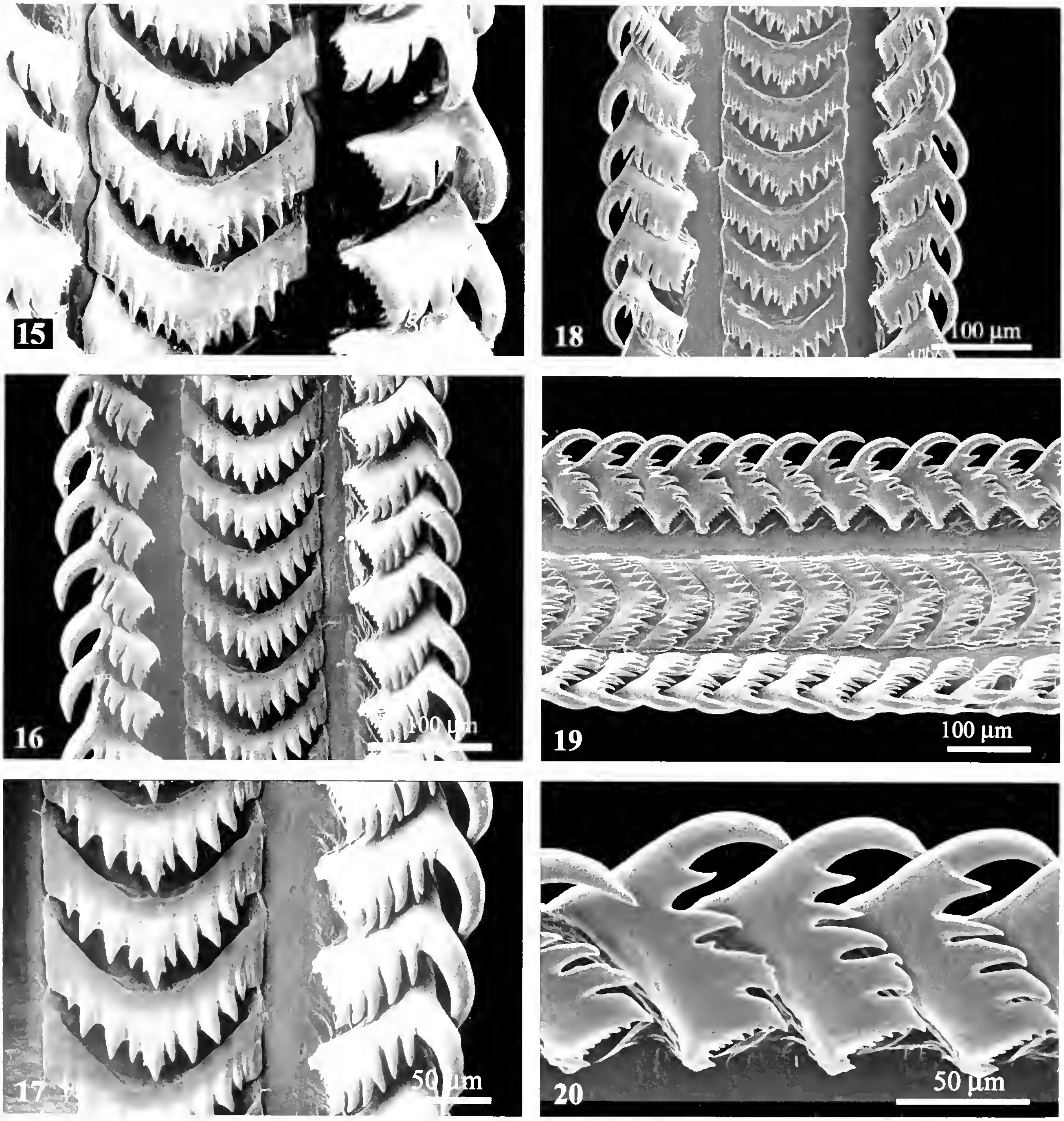
Periostracum smooth, tightly adhering to shell surface, color straw-olivaceous. Shell white beneath periostracum, with inconspicuous axial zigzag sinuous brownish lines, seen at dorsal shell surface, more pronounced immediately above the sulcus. Zigzag lines may be seen on apertural surface of shell, as well as dorsally, although they are always better pronounced on latter. Sometimes these lines are reduced to oblique dots above sulcus.

Operculum (figure 14) elongate-oval, occupying slightly more than ½ of the aperture length (including the canal), yellow, semitransparent, with terminal, clockwise-coiling nucleus. Growth lines numerous and thickened. See table 1 for shell measurements.

Anatomy: Morphology of one female specimen from Phan Ri River (figures 5–7) was examined. Due to its state of preservation, we were not able to study anatomy

←

dorsal and **7.** oblique dorsal views. ZMMU Le-25171. SL = 14.9 mm. Arrow indicate the basal sulcus. **8.** Apertural view. Natal Museum, L5452/T1764, SL = 14.2 mm. **9.** Apertural view. Natal Museum, L5452/T1764. SL = 13.0 mm. **10–13.** *Nassodonta insignis* H. Adams, 1867, holotype, the Natural History Museum, London (BMNH 1878.1.28.428). **10.** Apertural, **11.** right lateral, **12.** dorsal, and **13.** oblique dorsal views. Arrow indicate the basal sulcus. All shells at the same scale.



Figures 15–20. Radulae of *Nassodonta dorri*. **15.** Dorsal view of mid-portion of radula of figured syntype MNHN. **16–17.** Dorsal view of mid-portion of radula of syntype MNHN. **18–20.** Radula of the specimen on Figs. 5–7, ZMMU Lc-25171. **18.** Dorsal view of mid-portion. **19.** Right lateral (45°) view. **20.** Lateral view of lateral teeth to show indentation on inner side.

in detail. The rear of the foot possesses small, paired tentacles, although in preserved specimens these were much contracted. Head with medium long conical tentacles with large black eyes at their bases. Anterior part of the foot is pigmented with small widely spaced black speckles, while the mantle is heavily pigmented.

Proboscis in the retracted position is 1.2 mm long (0.28 SL) and 1.3 mm wide, poorly pigmented. Salivary glands paired, not fused, medium-sized. Valve of Leiblein small, pronounced. Mid- and posterior oesophagus was too poorly preserved for study.

Radula of figured syntype (figure 15) 3.5 mm long (0.25 SL and 0.34 AL), 350 µm wide (0.025 SL and 0.034 AL), composed of about 75 rows of teeth. Lateral

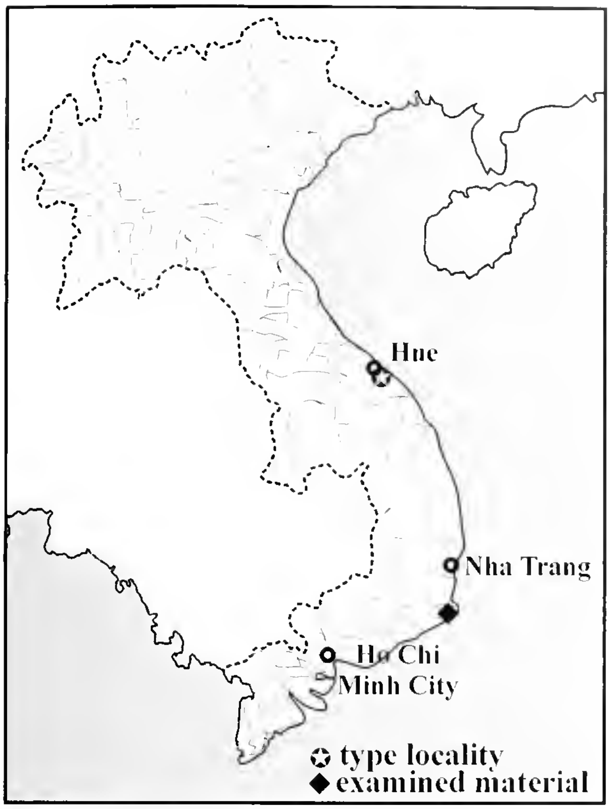


Figure 21. Distribution of *Nassodonta dorri* in Vietnam.

teeth with 4–6 cusps (number of cusps varies even on adjacent rows), outermost cusp ~ 2.5 times longer than innermost. Intermediate cusps either sharply pointed or bifurcating at their tips. Innermost cusp with 7–8 denticles on its lateral side. Rachidian with 11–12 cusps, central cusp serrated (number of cusps variable even on adjacent rows). Basal plate evenly and deeply notched along anterior edge.

Radula of second syntype (figures 16–17) 3.9 mm long (0.33 SL and 0.35 AL), ~ 350 μm (0.029 SL and 0.032 AL), composed of 73 rows of teeth, 1.5 nascent. Shape of teeth is very similar to that of figured syntype. The specimen from Phan Ri (shell on figures 5–7) have very similar radula (figures 18–20), 1.7 mm long (0.32 SL and 0.14 AL), ~ 355 μm wide (0.021 SL and 0.033 AL), composed of 85 rows of teeth, 3 nascent.

Variability (Table 1): Species fairly uniform in shell shape. The figured syntype differs from all other specimens examined in having a more swollen last whorl and in the complete absence of thickening of the outer lip above the edge of aperture. Although fairly large, this specimen appears to us to be immature, from its thin and still simple lip. Morphology of the upper part of the aperture suggests that the thickening of the lip is in its initial stages, whereas in the other specimens examined it is formed at the end of shell growth.

All other available specimens are much alike. The most variable character is the degree of thickening of the outer lip mentioned above. Zigzag lines may be seen on the apertural surface of the shell, as well as on shell dorsum, although they are always more pronounced on the latter. Sometimes these lines are reduced to oblique dots above the sulcus.

Remarks: The main differences between *N. dorri* and *N. insignis* (figures 10–13) (including *N. gravelyi*) are the much lower spire of the former, presence of strong axial nodules, shouldered whorls, strong constriction in the base of the outer lip, the smooth outer lip and the lack of a parietal nodule.

DISCUSSION

The species under consideration was originally described in the genus *Canidia* H. Adams, 1862. Type species (by monotypy) *C. fusca* H. Adams, 1862. The name *Canidia* appeared to be twice preoccupied. Cossmann (1901) proposed the substitute name *Ancutome*. *Ancutome* is

Table 1. Shell measurements (mm) of *Nassodonta dorri*

Character	Figured syntype	Syntype 2	Range	Average	σ
Shell length (SL)	14.4	12.0	12.0–14.9	13.69	0.93
Body whorl length (BWL)	11.6	11.0	10.6–12.8	11.61	0.64
Aperture length (AL)	10.3	9.7	8.7–10.8	9.86	0.73
Shell width (SW)	9.5	8.0	8.0–9.6	8.86	0.61
BWL/SL	0.82	0.92	0.81–0.94	0.85	0.04
AL/SL	0.73	0.81	0.70–0.81	0.72	0.04
SW/SL	0.67	0.67	0.61–0.67	0.65	0.02
Number of spiral ridges between fasciole and basal groove	2	1 very weak	1–3	2.42	0.32
Number of axial ribs on first teleoconch whorl	10	?	9–12	9.2	1.1
Number of axial ribs on second teleoconch whorl	12	?	9–13	10.7	1.26

generally considered to be at most a subgenus of *Clea* A. Adams, 1855 (e.g., Thiele, 1929). The type species, *Canidia fusca*, was never illustrated, and the location of its type material is unknown. Two specimens (suspected syntypes) from Cambodia, identified as "*C. fusca*" from the Cuming collection are stored in the collections of BM(NH), no. 20001316, and were examined by the authors. Nevertheless, they do not match the original description and therefore are not types. Thus the real position of *Canidia* remains unclear. The other species that was originally attributed to the genus is *Melanopsis helenae* Meder, 1847, which clearly belongs to *Clea*.

Therefore, allocation of *dorri* in the genus *Clea* (*Anentome*) (= *Canidia*) is certainly wrong. At the same time, the shell morphology is very similar to that of *Nassodonta insignis* H. Adams, 1867, including such an unusual character as the basal sulcus. This induces us to attribute the species to *Nassodonta* with some certainty.

This is the first confirmed record of genus *Nassodonta* outside Indian waters, despite the original type locality of China given for *N. insignis*. According to Dr. Thach the species is abundant in rivers of central Vietnam around Nha Trang and Phan Rang. Although *N. dorri* (like *N. insignis*) appears to inhabit the lower parts of these rivers and is probably found in brackish waters, the salinity of its habitat needs to be investigated.

The only other Asian species of the family Nassariidae known to inhabit fresh or brackish waters, are *Nassarius* (*Pygmaenassa*) *subconstrictus* (Sowerby, 1899), *N.* (*P.*) *orissaensis* (Preston, 1914) and *N.* (*P.*) *fossae* (Preston, 1915) from Lake Chilka and other Indian backwaters (see Cernohorsky, 1984).

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Systematics and ecology of *Gastrocopta (Gastrocopta) rogersensis* (Gastropoda: Pupillidae), a new species of land snail from the Midwest of the United States of America

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ABSTRACT

Gastrocopta rogersensis, a new species of recent gastropod mollusk (Pupillidae, Gastrocoptinae) is described from the vicinity of the Ozark Uplift and Paleozoic Plateau ("Driftless Area") in the midwestern USA. The structure of the angulo-parietal "tooth" in *G. rogersensis* consists of two discrete subparallel lamellae borne on a rectangular callus, distinguishing it from all *Gastrocopta procera* (Gould, 1840) subspecies and variants, including *Gastrocopta procera mcclungi* (Hanna and Johnston, 1913), *Gastrocopta procera riparia* (Pilsbry, 1912) and *Gastrocopta procera sterkiana* (Pilsbry, 1912). Morphometric analyses demonstrate that even at sites of co-occurrence, *G. rogersensis* shells are significantly ($P<0.0005$) smaller than *G. procera*. Additionally, while *G. rogersensis* exhibits no variation in shell size with latitude ($P = 0.876$), a highly significant ($P<0.0005$) clinal variation exists in *G. procera*. *G. rogersensis* populations appear restricted to undisturbed calcareous bedrock outcrops in areas that escaped Wisconsinan glaciation. The limited range, habitat specificity, and potential fire sensitivity of this species suggests that it should be given a high priority for conservation.

Additional key words: *Gastrocopta procera*, morphometrics, biogeography, ecology, midwestern USA.

INTRODUCTION

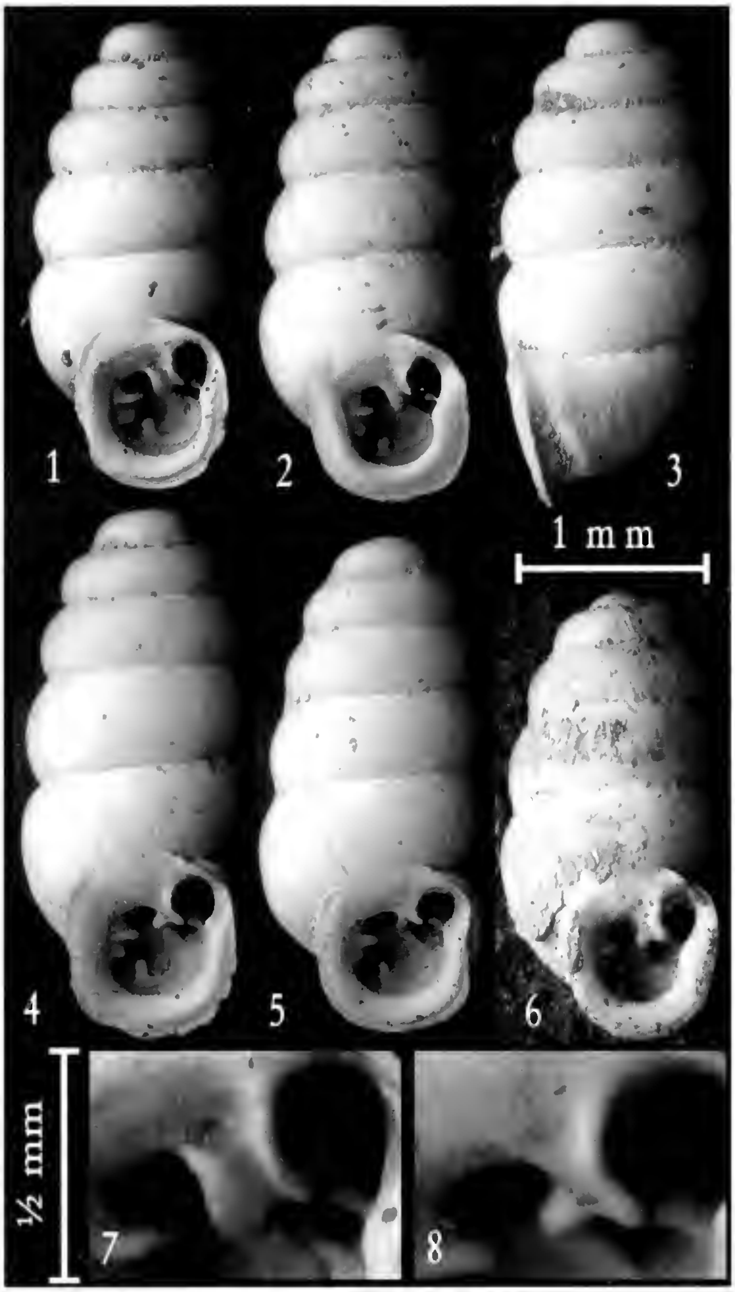
The genus *Gastrocopta* (Wollaston, 1878) comprises a group of pupillid mollusks of nearly global distribution (Pilsbry, 1948). In the Americas, this genus extends into the nearctic where at least 18 recent species occur east of the continental divide (Hubricht, 1985). Because of variability in apertural dentition and shell size, *Gastrocopta (Gastrocopta) procera* is one of the most taxonomically challenging members of this group. Pilsbry (1912, 1948) regarded *G. procera* to consist of four weakly differentiated taxa: *G. procera*, *Gastrocopta procera mcclungi*, *Gastrocopta procera sterkiana*, and *Gastrocopta procera* form *riparia*. However, Hubricht (1977) considered *G. p. mcclungi* synonymous with *G. procera* and elevated the remaining two forms to specific rank. Unfortunately, no data was presented to support these conclusions.

During studies on the recent land mollusks of the midwestern USA, we located 19 *Gastrocopta* populations from Arkansas, Illinois, Iowa, and Missouri that could be readily distinguished from *Gastrocopta procera* and its subspecies via a consistent suite of characteristics, even at sites of co-occurrence. An additional 10 populations of this form were documented from northwestern Illinois and southwestern Wisconsin through examination of *G. procera* material at the Field Museum of Natural History (FMNH). Inspection of *G. procera* material from the Academy of Natural Sciences of Philadelphia (ANSP) revealed that a specimen from Rogers, Arkansas also represented this form. This specimen had previously been identified and illustrated as *Gastrocopta procera mcclungi* (Pilsbry, 1948, figs 493:4–5). Pilsbry (1948) did not specifically discuss this specimen, even though conspicuous differences can be seen between it and the other illustrated *G. p. mcclungi* specimen (op. cit., figs 493: 1–3), which was stated by him to be "identical" to the type.

In this paper we describe these distinct populations as *Gastrocopta rogersensis* new species and comment on its relationship to the *Gastrocopta procera* complex, morphometrically compare it to *G. procera*, and consider its biogeography and ecology.

MATERIALS AND METHODS

Study Populations: All populations of *Gastrocopta* collected by the authors from the central USA were examined. Specimens of *Gastrocopta procera* sensu lato at FMNH and ANSP were also examined. Included in these were the Pilsbry (1948) figured specimens of *Gastrocopta procera mcclungi* from Rogers, Arkansas and South Dakota. Additionally, the holotype of *G. p. mcclungi* (USNM 226395) was examined.



Figures 1–8. Scanning electron micrographs of *Gastrocopta rogersensis* and *Gastrocopta procera*. **1, 3.** *Gastrocopta rogersensis*, UWGB 3914, Fults Hill Prairie Nature Preserve, Monroe County, Illinois, USA (90°11′15″ W, 38°9′19″ N). **2.** *Gastrocopta rogersensis*, UWGB 1061, Maquoketa South Glade, Clinton County, Iowa, USA (90°39′5″ W, 42°1′12″ N). **4.** *Gastrocopta procera*, UWGB 3916, Fults Hill Prairie Nature Preserve, Monroe County, Illinois, USA (90°11′15″ W, 38°9′19″ N). **5.** *Gastrocopta procera*, UWGB 575, Juniper Hill Shale Glade, Floyd County, Iowa, USA (92°59′2″ W, 43°3′10″ N). **6.** *Gastrocopta procera mcclungi*, holotype, USNM 226395, Long Island, Phelps County, Kansas. **7.** *Gastrocopta rogersensis*, angulo-parietal lamella, UWGB 3914, Fults Hill Prairie Nature Preserve, Monroe County, Illinois, USA (90°11′15″ W, 38°9′19″ N). **8.** *Gastrocopta procera*, angulo-parietal lamella, UWGB 3916, Fults Hill Prairie Nature Preserve, Monroe County, Illinois, USA (90°11′15″ W, 38°9′19″ N).

Morphometric analyses: Individuals were assigned to either *Gastrocopta* new species or *Gastrocopta procera* based on apertural lamella configuration. Twenty-five *Gastrocopta* new species and 24 *G. procera* populations from the states of Arkansas, Illinois, Iowa, and Wisconsin were used for shell morphometric analysis (table 1). Included were all 9 known stations at which these taxa co-occurred. The geographic coordinates for each population was determined using a Trimble hand-held GPS, appropriate USGS 7.5 minute topographic maps or DeLorme Gazetteer, and converted to UTM Zone 16 coordinates using ARC/INFO.

Table 1. Location and collection information for known *Gastrocopta rogersensis* sites and measured *Gastrocopta procera* sites with numbers of shells used in morphometric analyses. An X represents known *G. rogersensis* sites from where no specimens were measured.

Site	Location	Collector	Collection number	# Measured: *G. rogersensis*	# Measured: *G. procera*
Arkansas					
Baxter County					
Norfork	92°16'44" W, 36°13'22" N	Brian Coles	1996.6.2.3	10	
Salesville	92°16'52" W, 36°13'02" N	Brian Coles	1996.5.10.1	73	
Benton County					
Rogers		Pilsbry 1948	Figure 493.4-5	X	
Boone County	93°06'00" W, 36°29'00" N	George Walsh		X	
Carroll County					
Beaver Dam	94°01'36" W, 36°19'59" N	Brian Coles	1995.10.12.2	32	
Table Rock Lake	93°46'18" W, 36°28'22" N	Brian Coles	1998.6.6.1		4
Independence County					
Cushman N	91°47'27" W, 35°53'58" N	Brian Coles	1998.4.19.2		13
Izard County					
Calico Rock East	92°08'14" W, 36°06'48" N	Brian Coles		X	
Calico Rock West	92°08'55" W, 36°07'01" N	Brian Coles	1995.8.5.3	24	33
Madison County					
Withrow Springs Park	93°43'55" W, 36°09'07" N	Brian Coles	1995.10.13.2	4	2
Searcy County					
Harriet E	92°29'42" W, 35°59'08" N	Brian Coles	1999.10.24.2		1
Leslie S	92°33'19" W, 35°49'15" N	Brian Coles	1998.5.13.1		2
Marshall NW	92°41'39" W, 35°57'51" N	Brian Coles	1998.5.16.2		3
Marshall S	92°35'41" W, 35°54'21" N	Brian Coles	1998.5.31.2		12
Stone County					
Allison	92°07'23" W, 35°56'35" N	Brian Coles		X	
Barfoot Recreation Area	92°15'18" W, 36°01'16" N	Brian Coles	1997.7.12.2	2	
Calico Rock South	92°08'30" W, 36°06'22" N	Brian Coles	1997.7.17.2	1	2
South Side S	91°36'46" W, 35°40'00" N	Brian Coles	1999.4.4.4		6
Illinois					
Calhoun County					
Franklin Hill	90°36'38" W, 39°03'57" N	Jeff Nekola	UWGB 3868		42
Jackson County					
Kings Ferry Bluff	89°26'15" W, 37°36'02" N	Jeff Nekola	UWGB 3846		37
JoDaviess County					
Elizabeth	90°09'18" W, 42°19'59" N	John Slapcinsky	FMNH 286835	1	
Madison County					
Alton	90°13'36" W, 38°54'51" N	Jeff Nekola	UWGB 4311		31
Monroe County					
Fountain Gap	90°15'33" W, 38°22'36" N	Jeff Nekola	UWGB 3939	25	
Fults Reserve	90°11'15" W, 38°09'19" N	Jeff Nekola	UWGB 3914, UWGB 3916	45	42
Randolph County					
Chester	89°53'06" W, 38°56'42" N	Jeff Nekola	UWGB 4267, UWGB 4269	9	1
Prairie du Rocher	90°11'56" W, 38°06'28" N	Jeff Nekola	UWGB 3894, UWGB 3896	43	24
Iowa					
Allamakee County					
Fish Farm Mounds	91°17'11" W, 43°27'12" N	Jeff Nekola	UWGB 5366, 5368	5	–

Table 1. Continued

Site	Location	Collector	Collection number	# Measured *G. rogersensis*	# Measured *G. procera*
Clayton County					
Turkey River Mounds	91°02'11" W, 42°42'45" N	Jeff Nekola	UWGB 6468		47
Clinton County					
Maquoketa South	90°39'05" W, 42°01'12" N	Jeff Nekola	UWGB 6142	31	
Dubuque County					
Roosevelt Road	90°44'30" W, 43°32'55" N	Jeff Nekola	UWGB 3783	18	
Floyd County					
Juniper Hill Shale Glade	92°59'02" W, 43°03'10" N	Jeff Nekola	UWGB 575		11
Jackson County					
Hamilton Glade	90°34'08" W, 42°04'23" N	Jeff Nekola	UWGB 3732	16	
Winneshiek County					
Decorah Glade	91°46'10" W, 43°18'55" N	Jeff Nekola	UWGB 6315		17
Missouri					
Taney County					
Hollister	93°13'41" W, 36°37'00" N	Brian Coles		8	
Wisconsin					
Buffalo County					
Landfill Road	91°52'45" W, 44°15'56" N	James Theler	FMNH 285717		1
Crawford County					
Leitner Hollow	91°05'05" W, 43°13'03" N	James Theler	FMNH 286076	8	3
Rush Creek	91°07'54" W, 43°21'56" N	James Theler	FMNH 285824	6	
Grant County					
Dewey Heights	91°01'14" W, 42°44'03" N	James Theler	FMNH 286131	8	
Zimmer	91°02'50" W, 42°50'30" N	James Theler	FMNH 285680	11	
LaCrosse County					
Experimental Farm	91°00'47" W, 43°50'12" N	James Theler	FMNH 285670	8	
Hixon	91°12'00" W, 43°49'14" N	James Theler	FMNH 285761	8	
Pierce County					
Hager City	92°31'36" W, 44°36'20" N	James Theler	FMNH 285920		3
Trempealeau County					
Brady's Bluff	91°28'59" W, 44°01'12" N	James Theler	FMNH 285730	13	
Vernon County					
Battle Bluff	91°12'38" W, 43°27'36" N	James Theler	FMNH 286049	8	
Victor	91°12'45" W, 43°29'26" N	James Theler	FMNH 285843	1	4

For small populations (<40 individuals) all mature, undamaged shells were measured. For larger populations, a random sample of approximately 45 undamaged, adult shells was selected. Shell height and width was measured in increments of 0.01 mm using a dissecting microscope with a calibrated ocular micrometer. Maximum dimensions were recorded for each shell. Shell height was measured from the tip of the protoconch to the base of the lip, while shell width was measured from the right-most margin of the aperture to the left-most margin of the body whorl.

Differences in shell height and width for both *Gastrocopta* new species and *Gastrocopta procera* were analyzed via full 2-way ANOVAs in which taxon and geographic location served as independent variables. Because of natural groupings in occurrence, populations

were assigned to one of three geographic regions: Paleozoic Plateau, southern Illinois, or Ozarks. Differences in shell height and width within the 9 sites of co-occurrence were also documented using full 2-way ANOVAs in which taxon and site served as the independent variables.

The central tendencies in these relationships were graphically represented via box plots. In box plots, the central line represents the median of the sample, the margins of the box represent the interquartile distances, and the fences represent 1.5 times the interquartile distances. For data having a Gaussian distribution, approximately 99.3% of the data will fall inside of the fences (Velleman and Hoaglin, 1981). Outliers falling outside of the fences are shown with asterisks.

The strength of clinal variation in shell height vs. latitude (as expressed in UTM Zone 16 coordinates) was estimated for both species using least-squares linear regression. UTM coordinates were used to preclude potential bias originating from use of polar-coordinate latitude coordinates.

Scanning electron microscopy: Scanning electron micrographs of *Gastrocopta rogersensis* and *Gastrocopta procera*, taken with a Hitachi S-2460N Scanning Electron Microscope in N-SEM Mode (10 Pa; 22 kV) with a backscatter detector and no. 2 gamma correction.

Habitat associations: The physical habitat and associated plant communities were noted during field collection of sites documented by the authors. This information was determined for other sites through museum records and/or the published literature (e.g., Theler, 1997).

SYSTEMATICS AND DISCUSSION

Family Pupillidae Turton, 1831
Subfamily Gastrocoptinae Pilsbry, 1918
Genus *Gastrocopta* Wollaston, 1878
Subgenus *Gastrocopta* Wollaston, 1878

Gastrocopta rogersensis new species
(Figures 1–3)

Gastrocopta procera mcclungi Pilsbry, 1948, figure [plate] 493, in part, only specimen in figures 4–5.

Diagnosis: *Gastrocopta rogersensis* is similar in form to *Gastrocopta procera* but is distinguished by the shape of the angulo-parietal lamella. In *G. rogersensis* the angular and parietal lobes form two discrete, offset, sub-parallel ridges borne on a rectangular callus (figures 1, 2, 7). In *G. procera* these two lobes converge, creating a triangular structure (figures 4, 5, 8).

Description: Shell elongate-ovoid with a weakly conical spire, brown, weakly striate, 1.77–2.58 mm tall (mean = 2.11 mm) × 0.81–1.05 mm wide (mean = 0.92 mm); 6 whorls, the last 2 of approximately equal width; suture pronounced. The aperture is elongate and rounded with a non-continuous peristome. The weakly reflected lip is of lighter color than the rest of the shell, and is strongly reinforced with a shallow sulcus immediately behind. The aperture has 5 lamellae. The angulo-parietal consists of two discrete, approximately straight, sub-parallel lamellae borne on a rectangular callus with the angular portion originating near the junction of lip and body whorl. The columellar lamella is bilobed, the upper prominent and the lower nodular. The upper palatal lamella is short and placed in front of the angulo-parietal. The lower palatal is long and deeply inserted behind the angulo-parietal. The basal lamella is short, columnar, and inserted in front of the angulo-parietal.

Type material: Holotype (figures 1–3), FMNH 296651, 2.16 mm length × 0.96 mm width, Jeff Nekola leg. 11 Jul. 1998. Paratypes: FMNH 296657, 20 specimens collected with the holotype at Fults Hill Prairie Nature Preserve, Jeff Nekola leg.; Florida Museum of Natural History 285352, 5 specimens collected with the holotype at Fults Hill Prairie Nature Preserve, John Slapcinsky leg.; FMNH 296558, 10 specimens, Calico Rock West, Izard County, Arkansas (92°8′55″ W, 36°7′1″ N), Brian Coles leg; FMNH 296559, 10 specimens, Salesville, Baxter County, Arkansas (92°16′52″ W, 36°13′2″ N), Brian Coles leg.; FMNH 296660, 10 specimens, Prairie du Rocher, Randolph County, Illinois (90°1′56″ W, 38°6′28″ N), Jeff Nekola leg.; FMNH 296661, 10 specimens, Maquoketa South Glade, Clinton County, Iowa (90°39′5″ W, 42°1′12″ N), Jeff Nekola leg. FMNH 285730, 13 specimens, Brady's Bluff, Trempealeau County, Wisconsin (91°28′59″ W, 44°1′12″ N), James Theler leg.

Type locality: Fults Hill Prairie Nature Preserve (90°11′15″ W, 38°9′19″ N), Monroe County, Illinois, USA, approximately 3 km SE of Fults along Bluff Road on dry limestone outcrops, under Red Cedar (*Juniperus virginiana* L.) at the crest of a bluff. We selected this locality as it is centrally located within the known range of *Gastrocopta rogersensis*, and exists within a protected natural area. Additionally, the locality is included in part of the range of *G. rogersensis* where the new species occurs sympatrically with *Gastrocopta procera*.

Etymology: The specific name honors the town of Rogers, Arkansas. This is the collection location for the specimen upon which the first published illustration was based. Even though we have been unable to relocate them in Rogers, extant populations are known within 40 km at Withrow Springs State Park and Beaver Dam.

Subgeneric allocation: The approximately straight angulo-parietal lobes as seen in basal view, columnar basal lamella, and brown shell color indicate that *Gastrocopta rogersensis* belongs in the subgenus *Gastrocopta*. Superficially, its angulo-parietal lamella resembles that of several species in *Gastrocopta* subgenus *Immersidens*, notably *Gastrocopta bilamellata* (Sterki and Clapp, 1909) and *Gastrocopta dalliana* (Sterki, 18[illegible]) (Pilsbry, 1948: figure 490: 1–1[illegible]). However, [illegible]

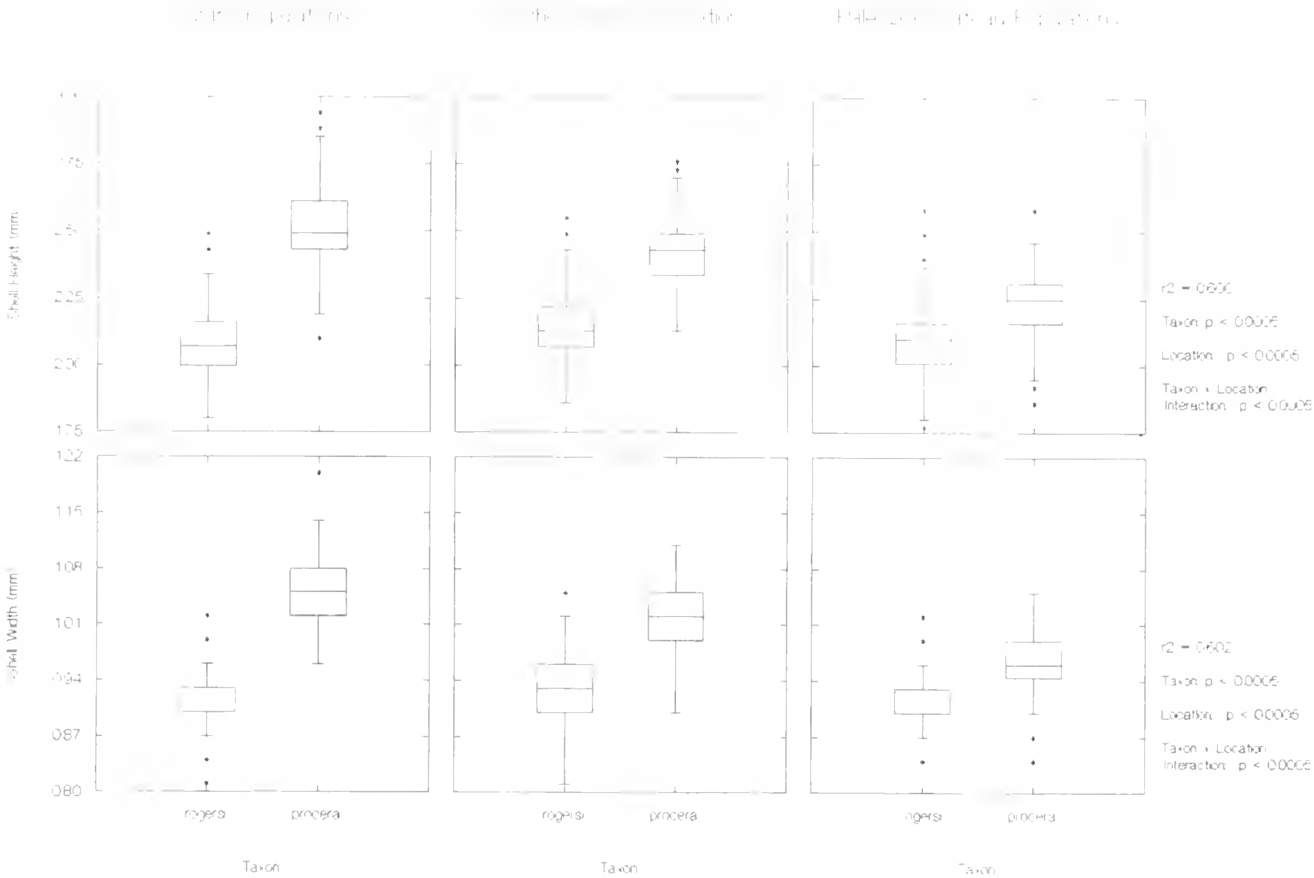


Figure 9. Box-plot diagram of variation in *Gastrocopta rogersensis* and *Gastrocopta procera* shell height and width within the Ozarks, southern Illinois, and Paleozoic Plateau. Statistical results are based on a 2-way ANOVA with interaction.

this subgenus are characterized by having angular and parietal lobes that are curved or bent at their distal ends, an elongate basal lamella whose long axis is parallel to the lip, and a clear to white shell color.

Morphometrics: Shells from 414 *Gastrocopta rogersensis* (146 from Paleozoic Plateau populations, 121 from southern Illinois, 147 from the Ozarks), and 343 *Gastrocopta procera* (88 from Paleozoic Plateau populations, 177 from southern Illinois, 78 from the Ozarks) were measured. Comparison of these demonstrated that *G. rogersensis* averaged 2.11 mm in height whereas *G. procera* averaged 2.40 mm (figure 9). This difference was highly significant ($P<0.0005$). Additionally, the difference in height between Ozark and southern Illinois populations was greater than for Paleozoic Plateau populations ($P<0.0005$). Similar trends were noted in shell width (Figure 3), with *G. rogersensis* averaging 0.92 mm and *G. procera* averaging 1.02 mm. This difference was highly significant ($P<0.0005$) and also varied between population centers ($P<0.0005$), with maximum divergence occurring in the Ozarks.

One-hundred and forty three of the measured *Gastrocopta rogersensis* and 113 of the measured *Gastrocopta procera* shells originated from sites of co-occurrence. When analyses were limited to these stations, highly significant differences ($P<0.0005$) were still noted in both shell height and width (figure 10). Additionally, a highly significant interaction between site and shell height ($P<0.0005$) and width ($P = 0.002$) was noted, with maximum divergence occurring between the two species in the Ozarks.

Linear regression of shell height vs. UTM N-S coordinates (table 2) demonstrated that while *Gastrocopta procera* shell height strongly ($r^2 = 0.375$) and significantly ($P<0.0005$) increased towards the south, no clinal variation occurred in *Gastrocopta rogersensis* ($P = 0.876$; $r^2 = 0.000$). Because of this, differences in shell size are less marked between *G. rogersensis* and *Gastrocopta procera* in the north. It is not clear why these taxa respond differently to identical environmental gradients.

Geographic distribution: The 30 known stations for *Gastrocopta rogersensis* appear restricted to three distribution centers: the Ozark uplift of northern Arkansas and southern Missouri, southwestern Illinois, and the Paleozoic Plateau (or "Driftless Area"; see Prior, 1991) of northeastern Iowa, northwestern Illinois, and southwestern Wisconsin (figure 11). The majority of known sites in the Ozarks are restricted to limestone bluffs near the upper western (Benton, Carroll and Madison coun-

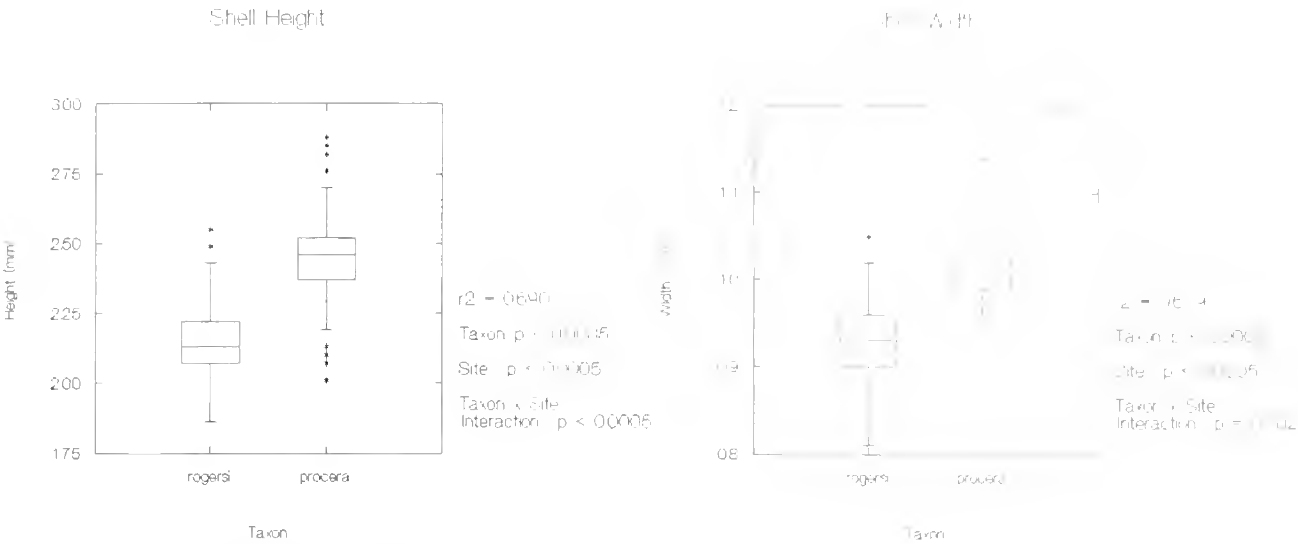


Figure 10. Box-plot diagram of variation in *Gastrocopta rogersensis* and *Gastrocopta procera* shell height and width within sites of co-occurrence. Statistical results are based on a 2-way ANOVA with interaction.

ties) and eastern (Baxter, Izard, and Stone counties) White River and its tributaries. In southwestern Illinois, *G. rogersensis* is limited to a 60 km extent of limestone bluffs along the Mississippi River in Randolph and Monroe counties. The Paleozoic Plateau populations lie within 50 km of the Mississippi River in Jo Daviess County (Illinois), Allamakee, Clinton, Dubuque, and Jackson counties (Iowa), and Crawford, Grand LaCrosse, Trempealeau, and Vernon counties (Wisconsin). The localized distribution of *G. rogersensis* contrasts markedly with *Gastrocopta procera procera*, which is widespread throughout much of the eastern and midwestern USA (Hubricht, 1985).

Even though we have documented land snails at over 700 sites in the region, as neither our own collections (nor those museum collections that we have examined) fully cover this landscape, we cannot unequivocally state that *G. rogersensis* is limited to only these three distributional centers. This is particularly true in the south, where undercollection in southern Missouri may well account for the apparent disjunction between Ozark and southern Illinois populations.

The dominant distribution for localized midwestern USA Polygyridae and Zonitidae species (Hubricht, 1985; Emberton, 1995) is typically centered on the northwestern Arkansas Ozarks [e.g., *Inflectarius edentatus* (Sampson, 1889), *Paravitrea simpsoni* (Pilsbry, 1889), *Stenotrema labrosum* (Bland, 1862), and *Ventridens brittsi* (Pilsbry, 1892)]. However, other localized midwestern distributions also exist [e.g., *Discus macclintocki* (F.C. Baker, 1928), *Euchemotrema hubrichti* (Pilsbry, 1940), and *Triodopsis discoidea* (Pilsbry, 1904)]. *Gastrocopta rogersensis* possesses one of these latter patterns, being limited to the Ozarks and the Paleozoic Plateau. Its range is most closely matched by that of *Vertigo meramecensis* VanDevender, 1979 which exhibits an almost identical distribution (Frest and Fay, 1981; Hubricht, 1985; Frest, 1991; author's unpublished data). Both of these regions are underlain by carbonate bedrock, have a rugged terrain, and escaped glaciation during the Wisconsinan. Unlike *G. rogersensis*, however, *V. meramecensis* is restricted to cool, mesic carbonate cliffs (Frest, 1991).

Table 2. Summary statistics for regression of shell height vs UTM N-S location for *Gastrocopta rogersensis* vs *Gastrocopta procera*. The best-fit slope is calculated as the mm change in shell height per 10^6 meters.

Species	*G. rogersensis*	*G. Procera*
n	415	343
slope	−0.003	−0.367
standard error	0.021	0.026
t	−0.156	−14.289
p (2-tailed)	0.876	<0.0005
r^2	0.000	0.375

Taxonomic remarks: Pilsbry (1948) differentiated forms and subspecies in the *Gastrocopta procera* group based primarily on the degree of separation of the angular and parietal portions of the angulo-parietal lamella grading from *Gastrocopta procera* form *riparia* (least separated) through *Gastrocopta procera procera* and *Gastrocopta procera sterkiana* to *Gastrocopta procera mcclungi* (most separated). *Gastrocopta p. mcclungi* was also thought to differ from the nominate species by being shorter and having a thicker and more convex lip (Baker, 1939; Franzen and Leonard, 1943; Pilsbry, 1948). Subsequent workers have considered *G. p. mcclungi* as simply a variant of *G. procera* (Leonard, 1959; Hubricht, 1985). Hubricht (1977, 1985) differentiated the remaining taxa as distinct species based primarily on the position and slope of the lo-

Figure 11. Distribution of *Gastrocopta rogersensis.*

tooth, ranging from *G. procera* (most deeply inserted) through *G. sterkiana* to *G. riparia* (least deeply inserted) but failed to give adequate reasoning for these conclusions. We have found these features to be highly variable, with continuous variation apparently existing both within and between populations. Further morphometric and taxonomic investigations will be necessary to help determine the appropriate taxonomic categories within this group.

Despite continued ambiguity over the status of forms within the *Gastrocopta procera* complex, *Gastrocopta rogersensis* new species is distinct in all aspects. It differs most conspicuously by having the angular portion of the angulo-parietal lamella arising near the lip and running parallel and separate from the more deeply set parietal portion. While the angular and parietal portions show a variable degree of distal separation in *G. procera*, in all cases they fuse at approximately mid-length. Sympatric populations of *G. rogersensis* and *G. procera* do not intergrade in this feature. Additionally, *G. rogersensis* individuals appear consistently smaller (ca. 0.25 mm) than *G. procera*. Less striking differences include the distinctly reflexed lip of *G. rogersensis* as seen in profile (figure 3), and its somewhat longer and more deeply inserted lower palatal lamella.

Based on these criteria, examination of the holotype of *Gastrocopta procera mcclungi* (USNM 226395, figure 6), and the ANSP figured specimen of *G. p. mcclungi* from South Dakota (Pilsbry, 1948, fig. 493: 1–3) revealed that both fell well within the normal range of variation for the *Gastrocopta procera* complex. Thus, we concur with Leonard (1959) and Hubricht (1985) that this taxon should be regarded as a synonym of *G. procera*. However, the figured ANSP specimen of *G. p. mcclungi* from Rogers, Arkansas (Pilsbry, 1948, fig. 493: 4–5) conforms in all respects to *Gastrocopta rogersensis*. The reasons for the overlooking of the uniqueness of this specimen by Pilsbry are likely two-fold: first, the specimen fell within his concept of *G. p. mcclungi* as it has a very pronounced separation between the angulo-parietal lobes. Second, as no other *G. rogersensis* specimens exist in the ANSP collections, there was only limited opportunity for him to observe the other consistent differences that exist between it and *G. procera*.

Because of this confusion, *Gastrocopta rogersensis* has remained undescribed even though specimens have likely existed in collections for over 60 years. Baker (1939) referred to *Gastrocopta procera mcclungi* from Illinois, within the known range of *G. rogersensis*. His drawings of this taxon appear similar to *G. rogersensis*, but are too crude for definitive confirmation. Hutchison (1989) listed *G. p. mcclungi* from Fountain Bluff in Jackson County, Illinois, approximately 35 km to the SE of the southern-most known Illinois *G. rogersensis* population. Even though we have not been able to examine these specimens, the reported location and habitat make it likely that these also represent *G. rogersensis*. Theler (1997) encountered *G. rogersensis* in his survey of western Wisconsin bedrock glade land snail faunas, but identified all individuals as *G. procera*.

Preferred habitats: All known populations of *Gastrocopta rogersensis* are limited to xeric or dry-mesic calcareous rock outcrops. Ozark and southern Illinois populations were encountered on wooded cliffs or cliff crests, as at the type location. The Paleozoic Plateau populations are restricted to bedrock glades (see Theler, 1997 for images of the Brady Bluff site). In these habitats, individuals are limited to organic accumulations in xeric, sparsely vegetated microsites, where short-statured grasses and forbs such as *Agoseris cuspidata* (Pursh.) Raf., *Andropogon scoparius* Michx., *Artemesia caudata* Michx., *Carex abdita* Bickn., *Carex richardsonii* R.Br.,

Castilleja sessiliflora Pursh, *Muhlenbergia cuspidata* (Nutt.) Rydb., and *Viola pedata* L. occur.

CONSERVATION RECOMMENDATIONS

Because of its limited geographic range and habitat specificity, *Gastrocopta rogersensis* should be considered of conservation importance. Even within its distributional centers, populations are sporadic and tend to be limited to high-quality sites. Ironically, a further concern for its continued survival is the occurrence of many populations (including the type and most of the Wisconsin stations) within managed nature reserves. Prairie and bedrock glade habitats throughout the midwest USA are generally subjected to intense fire management, as it has been believed that reintroduction of fire will increase the vigor and diversity of the grassland biota (e.g. Curtis, 1959; Pauly, 1985). Because of this, Theler (1997) stated that fire management is essential to maintain the habitats used by *G. rogersensis* in Wisconsin. However, fire is known to be deleterious to many native prairie plant (Hill and Platt, 1975) and arthropod (Swengel, 1996; Harper et. al, 2000) species. Such negative impacts likely also exist for *G. rogersensis*, as individuals reside in thatch and organic duff layers that are removed through repeated fire episodes. As recovery of these layers takes over a dozen years in xeric grasslands (Gibson and Hulbert, 1987), the frequent use of fire management (<10 year return intervals) may limit the amount of appropriate habitat and significantly reduce the size of *G. rogersensis* populations. Suggestions of this can be seen in Theler (1997), as the most frequently burned sites (e.g. Rush Creek) also have the smallest *G. rogersensis* and *G. procera* populations. The number of recovered shells per unit volume of soil litter in these managed Wisconsin sites is 2–3 times smaller than that observed in nearby unburned Iowa sites (e.g. Maquoketa South and Roosevelt Road). Such trends should not be surprising, as land snails are highly sensitive to fire (Frest and Johannes, 1995). We have observed 50% reductions in richness and order-of-magnitude reductions in abundance of land snails between adjacent unmanaged and fire-managed grasslands in northwestern Minnesota (author's unpublished data). Thus, overuse of fire management by conservation groups may pose as great of a threat to the survival of *G. rogersensis* as habitat loss.

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Book Review

Catalogue and Bibliography of the Marine Shell-bearing Mollusca of Japan. Type Figures.

Shun'ichi Higo, Paul Callomon, and Yoshihiro Goto 2001. Elle Scientific Publications, Osaka, 208 pp. $325.00.

This important work is now complete with the publication of the volume of figures. The text volume was reviewed in these pages (Petit, 1999) shortly after its publication. The book is unique in that all figured specimens are name-bearing types. As the authors state in the introduction, it became evident during the production of the text volume that the identity of many species was uncertain. As only type specimens are figured, readers may be assured that the figures match the names.

Almost 2000 type specimens are figured in color. Each page of figures comprises 16 excellent, informative illustrations. The arrangement of this data is, of course, explained in the introduction that should be read before the book is used. Data is arranged in five areas, the most important being the entry number that corresponds to the species number in the text volume. The suffix "s" on a number indicates that the name of the type figured is treated as a junior synonym in the text volume. As an example, there is a figure of the holotype of *Zafra mitriformis* A. Adams, 1860, and also three figures of type species of nomina that appear in most literature as synonyms of *Z. mitriformis*: *Z. zonata* (Gould, 1860), *Z. validicosta* (Habe, 1960), and *Z. subvitrea* (E. A. Smith, 1879). When viewed together it is clear that all four are not conspecific. On the other hand, the figures of *Buccinum midori* Habe and Ito, 1965, and *B. oedematum* Dall, 1907, appear to represent the same species. There are numerous examples to be found of both cases. This book dramatically illustrates the importance of having figures of type specimens.

The second bit of data is a scale bar used for specimens under 10 mm, and the third is a measurement in millimeters for larger specimens. Of little interest to the casual user is the fourth bit of information that is an indication used if the figure is a composite image. A composite image may be used for a shell whose shape precludes bringing the entire specimen into good focus at once, in which case two photographs are taken and combined.

The final bit of data is termed the "main data box" and contains the specific name and generic placement used in the text volume; the author and date of publication; type status; museum name and registration number. The rules for designation of type specimens have always been somewhat confusing and were recently made even more so by changes in the fourth edition of the ICZN. The authors list the various kinds of types recognized, the acronyms for which are used in the "main data box," and give a description of each.

The only negative aspect of this production is the fact that only some of the taxa listed in the text volume are represented by figures of type specimens. As explained by the authors, priority was given to species originally described from Japan as their limited resources precluded inclusion of all species. Many well-known Japanese species originally described from elsewhere by the earlier authors (Linnaeus, Gmelin, Lamarck, and others) are therefore absent.

An appendix lists additional species names for the Catalogue, errata for the Catalogue listings, errata and additions to the bibliography, and additional and emended Japanese names. There is a complete index. As with the first volume, this book of figures is superbly produced. It is A4 in size, the text printed on cream stock paper and the plates on heavy glossy stock, and bound in Damascene cloth with a gold-stamped leatherette spine. As is standard in Japan, it comes in a slipcase.

LITERATURE CITED

Petit, R. E. 1999. Book review. Catalogue and bibliography of the marine shell-bearing Mollusca of Japan. The Nautilus 113: 102.

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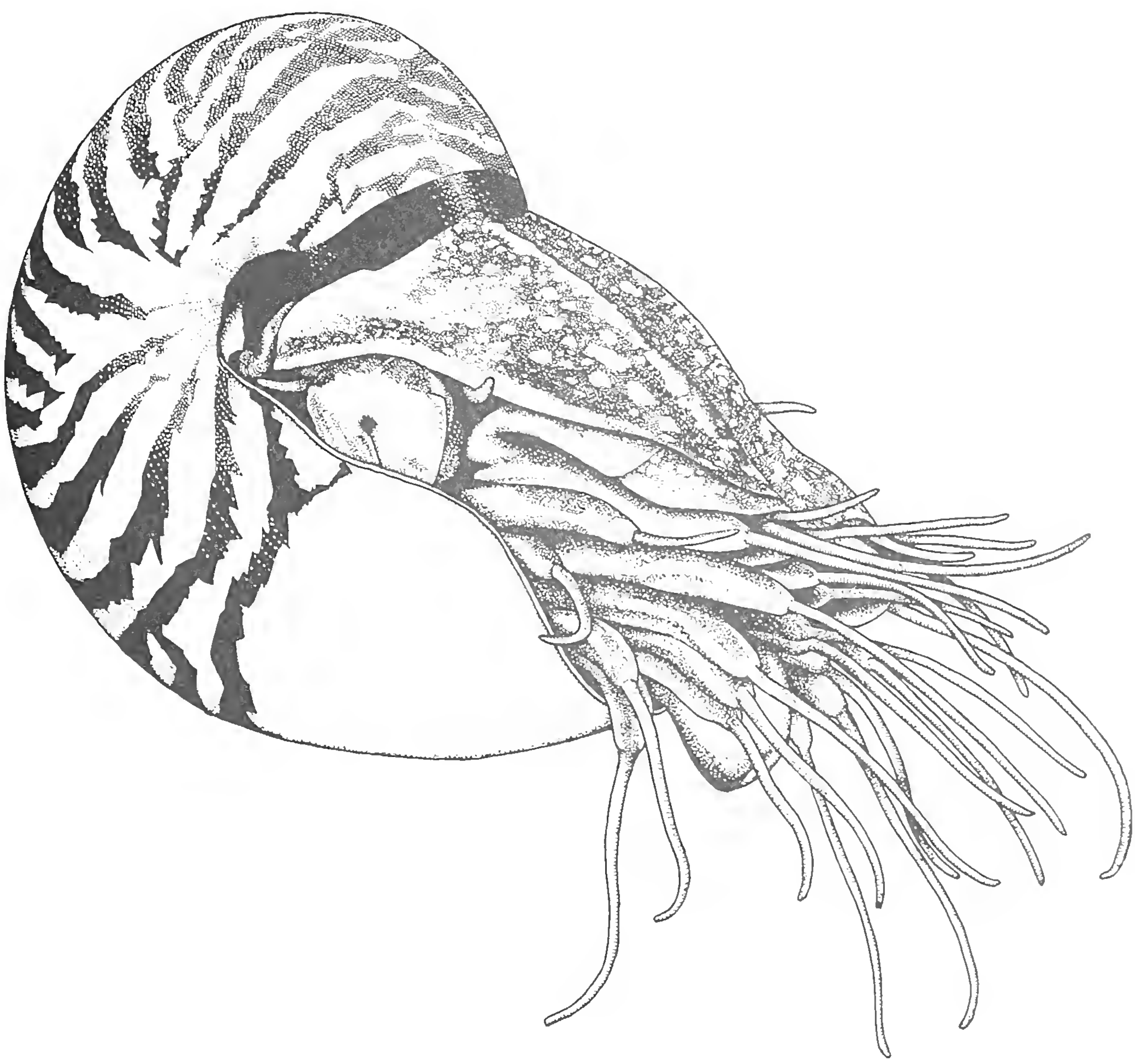

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New data on the taxonomy and distribution of the genus *Littoraria* Griffith and Pidgeon, 1834 (Gastropoda: Littorinidae) in Indo-West Pacific mangrove forests

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ABSTRACT

This paper adds new data on mangrove-associated species of *Littoraria* in the Indo-West Pacific region that have accumulated since the taxonomic revision of the group by Reid (1986a). One new species is described from the northeastern Indian Ocean and *L. sinensis* (Philippi, 1847) is distinguished from the similar *L. articulata* (Philippi, 1846) with which it was previously confused. Significant extensions to the distribution ranges of 12 species are reported. The penis, paraspermatozoa and radula of *L. delicatula* (Nevill, 1885) are described for the first time and additional information given on the geographical variation of *L. filosa* (Sowerby, 1832) in Australia. New literature (post-1985) on the entire genus *Littoraria* is briefly reviewed.

INTRODUCTION

The family Littorinidae is among the most well studied of marine gastropod groups, for it is of worldwide distribution and its members are usually abundant, accessible and easily collected in the intertidal zone (see reviews by McQuaid, 1996a, b). Until some 30 years ago the group was noted for a confused taxonomy based mainly on highly variable shell characters. However, since then the application of techniques of fine anatomy, scanning electron microscopy and molecular biology has resulted in refinement. Within the most well known subfamily, the intertidal and monophyletic Littorininae (Reid, 1989a), recent studies recognise 139 species in eight genera: 1 *Melarhaphe* (Rosewater, 1981; Reid, 1989a); 11 *Peasiella* (Reid, 1989b; Reid and Mak, 1998); 2 *Mainwaringia* (Reid, 1986b); 10 *Tectarius* (Rosewater, 1972; Reid and Geller, 1997); 1 *Cenchritis* (Rosewater, 1972; Reid, 1989a); 39 *Littoraria* (Reid, 1986a, 1999a, b, this study); 19 *Littorina* (Reid, 1996); and 56 *Nodilittorina* (Bandel and Kadolsky, 1982; Reid, 1989a, in press a, b). For the subfamily Littorininae there is at least a preliminary phylogeny of the genera (Reid, 1989a) and some species-level phylogenies (e.g. Reid et al., 1996; Reid, 1999b), and further molecular phylogenies are now being produced. For all these 139 species the reproductive mode and habitat are known, and for almost all of them the geographical distribution is recorded in detail. This, therefore, represents a remarkable dataset among marine invertebrates, a relatively well-worked monophyletic group of worldwide (but predominantly tropical) distribution. Once a more robust phylogenetic framework is achieved it should become a model system for the study of macroevolutionary processes (e.g. *Littorina*, Reid et al., 1996). Meanwhile, it is important to understand the systematics of these species accurately and to record their distributions as precisely as possible.

The modern concept of the genus *Littoraria* as a monophyletic group was established by Bandel and Kadolsky (1982) and Reid (1986a, 1989a); before this the species were generally included in *Littorina*, a large polyphyletic assemblage. The genus is almost exclusively tropical in distribution and the highest diversity is found in the Indo-West Pacific biogeographic region. At the species level, the classification of this group underwent a considerable change following a revision by Reid (1986a) of the Indo-Pacific species associated with mangrove habitats. Using a range of evidence from anatomy (in particular of penis, paraspermatozoa and pallial oviduct), radula, shell morphology, habitat, distribution, and copulation frequency, it was shown that 20 species could be discriminated whereas only 3 had been commonly distinguished previously. Since this revision, new collections have accumulated. As a result, some of the earlier conclusions must be revised and three additional species can be recognised in the region. The new material also adds significant extensions to the distributional ranges of some taxa. It is the aim of this paper to describe and redescribe two of the additional taxa (the third will be described elsewhere; Stuckey and Reid, in preparation) and to document some new observations and distributional records. It should be used in conjunction with the earlier work (Reid, 1986a).

At the time of Reid's (1986a) systematic revision, other aspects of the biology of these tropical species had

received relatively little study. However, in the years since then they have received much more attention. Among several remarkable features of *Littoraria* are the association of many species with mangrove trees, leading to studies of their zonation patterns, diet and predation. Some members are ovoviviparous, and many show spawning or feeding migrations with lunar and tidal periodicity. A striking color polymorphism of the shell is shown by species occurring on mangrove foliage and these have emerged as a model system for the study of the maintenance of polymorphism by natural selection. There has also been new work on ultrastructure, egg capsules, radular plasticity, parasitism and genetics. This new literature will be briefly reviewed here.

NEW LITERATURE ON *LITTORARIA* SINCE 1985

Reid (1986a, 1989a) listed 36 known species of *Littoraria* worldwide (one of which was unnamed), but detailed descriptions were restricted to those 20 found in association with mangrove trees in the Indo-West Pacific region. Since then the six species occurring in the Eastern Pacific region have been described (Reid, 1999a; see also Reid and Kaiser (2001) for two new records of Indo-West Pacific species in the eastern Pacific) including the unique nonplanktotrophic *L. aberrans* (Philippi, 1846) and the new taxon *L. rosewateri* Reid, 1999. In addition to the single new species described in the present paper, and the recognition of two taxa within '*L. articulata* (Philippi, 1846)' (as used by Reid, 1986a), a further new species from northern Australia is being described elsewhere (Stuckey and Reid, in preparation; see Warmoes et al., 1990, and Reid, 1992a, for additional regional taxonomic accounts). This brings the total for the genus to 39 species.

A preliminary phylogenetic analysis of all *Littoraria* species then known, based on cladistic analysis of morphological characters, was done by Reid (1986a). This has since been revised and updated (Reid, 1999b). The new phylogeny was not well resolved, but supported the monophyly of the subgenera *Palustorina* and *Littorinopsis*, and suggested that the subgenus *Littoraria* was a paraphyletic assemblage; a significant change to the phylogenetic classification of the genus was the combination of five mainly rock-dwelling Indo-Pacific species (*L. pintado* (Wood, 1828), *L. mauritiana* (Lamarck, 1822), *L. glabrata* (Philippi, 1846), *L. coccinea* (Gmelin, 1791), *L. undulata* (Gray, 1839)) in the basal subgenus *Protolittoraria* which had previously held only *L. pintado* (Reid, 1989a). The fossil record of *Littoraria* is limited, but better than that of other littorinid genera, probably because preservation is more likely in mangrove environments than on high-energy rocky shores. The known fossil species were listed by Reid (1999b) and discussed in the context of vicariant events in the biogeographic history of the clade. A similar history, of Tethyan origin and subsequent vicariance, has been proposed for mangroves by Ellison et al. (1999), who cited the worldwide diversity gradient of *Littoraria* species in support. Extinctions of marine invertebrates during historical time are rarely reported; *L. flammea* (Philippi, 1847) was included as one of only four possible examples among gastropods discussed by Carlton (1993).

Regrettably little genetic work has yet been undertaken on *Littoraria*. Several studies of allozyme variation within the Australian species have confirmed that the species defined by morphological criteria are indeed distinct (Johnson and Black, 1998; Schmidt, 1998; M. Stuckey, personal communication). Levels of intraspecific genetic variation have been assessed using allozyme markers in *L. angulifera* (Lamarck, 1822) (Janson, 1985) and in the two subspecies of *L. cingulata* (Philippi, 1846) (Johnson and Black, 1998). DNA sequences have so far been published for the 16S ribosomal RNA gene (3 species, Reid et al., 1996) and 18S rRNA gene (1 species, Winnepenninckx et al., 1998), but have yet to be used for phylogeny reconstruction within the genus. This should be a priority.

Although the genus *Littoraria* is well known as a characteristic inhabitant of mangrove forests, this is not true of all the species. There appears to have been an evolutionary specialisation to the mangrove habitat, since basal species occur exclusively on rocks, or on both rocks and driftwood, whereas only the more derived clades occur on trunks and foliage of mangrove trees (Reid, 1999b). The three-dimensional structure of the mangrove habitat, and frequent sympatric occurrence of several *Littoraria* species, has stimulated numerous accounts of comparative zonation patterns. These have been carried out in Australia and the western Pacific (Cook et al., 1985; Reid, 1985; Boneka, 1994; Catesby and McKillup, 1998), Japan (Ohgaki, 1992), the Caribbean (Gutierrez, 1988) and the eastern Pacific (Blanco et al., 1995, Blanco and Cantera, 1999; Cantera et al., 1999). In general, *Littoraria* species do not seem to be restricted to particular tree species, but are found on characteristic substrates (bark or foliage), at typical tidal heights and in typical horizontal zones (seaward or landward fringes) within the forest; furthermore, the assemblages of species on continental margins and on oceanic islands are different (Reid, 1985, 1986a, 1999a). Some of the typically mangrove-associated species can also be found on sheltered rocky shores, including *L. articulata* (see Crowe, 1997), *L. sinensis* (Philippi, 1847) (accounts of distribution of '*Littorina scabra*' on rocky shores of Hong Kong and southern China probably refer to a mixture of these two species, e.g. Ohgaki, 1985, Yi and Li, 1988, You, 1990) and *L. flava* (King and Broderip, 1832) (Montinho and Alves-Costa, 2000). Ecological data on those species that are found mainly on rocks and driftwood, such as *L. undulata* and *L. coccinea*, are scarce (Poulicek et al., 1994; Sacchi, 1994; Ohgaki, 1998).

Within the mangrove environment those species inhabiting trunks and roots at lower levels on the trees migrate vertically with the tide in order to remain above the water level (Yipp, 1985; Gutierrez, 1988, Ohgaki, 1992; Jensen, 2000). Similar behavior has been reported on rocky shores (Ohgaki, 1993; Svane and Pringgenies,

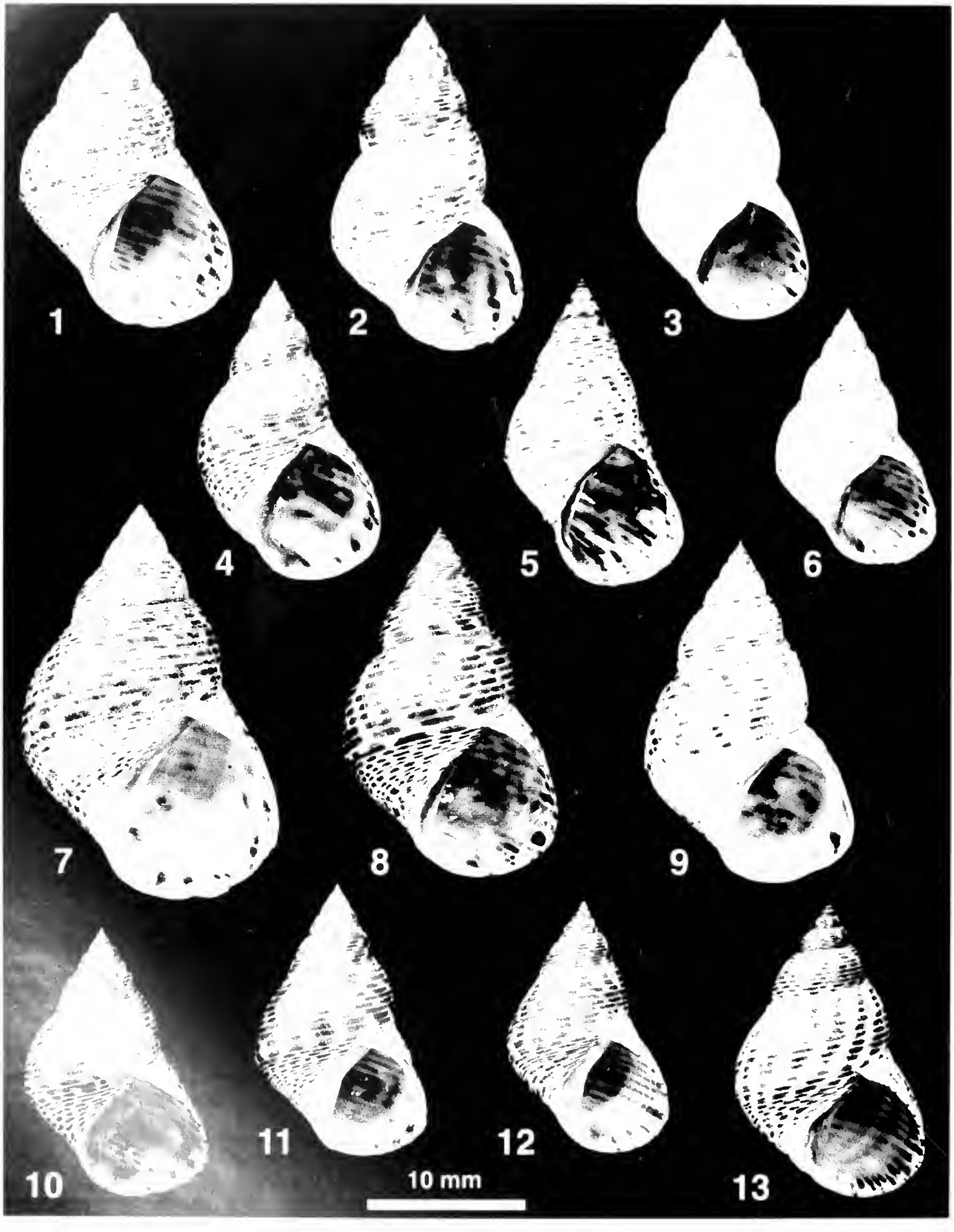
1997) and displacement experiments have been carried out (Antwi and Ameyaw-Akumfi, 1987). In contrast, species typically found at higher levels among the foliage of mangroves are not contacted by the high tide, but become active during rain and heavy dew (Little and Stirling, 1984; Kohlmeyer and Bebout, 1986; Ohgaki, 1992). *Littoraria irrorata* (Say, 1822) occurs in salt marshes in the southeastern United States, where it climbs the stems of marsh grass and descends to feed on the substrate at low tide. This behavior has been investigated in relation to both thermoregulation (McBride et al., 1989; Williams and Appel, 1989; Henry et al., 1993) and avoidance of predators (Warren, 1985; Vaughn and Fischer, 1988, 1992; Dix and Hamilton, 1993; Duval et al., 1994). This species has been employed in studies of trail following (Stirling and Hamilton, 1986; Tankersley, 1989, 1990; Robbins and Hamilton, 1996). Unlike all other species of the genus, it is entirely temperate in distribution and hibernates during winter (Paul et al., 1989). Aggregation behavior has been described in *L. flava* on rocky shores in Brazil (Montinho and Alves-Costa, 2000).

Littoraria species suffer high levels of predation, apparently mainly from aquatic predators, accounting for their avoidance of submersion by the rising tide. In mangrove forests portunid crabs take snails at and below the water surface, while some grapsids are able to climb several metres up into the trees (Maruthamuthu et al., 1985, 1986; Borjesson and Szelistowski, 1989; Reid, 1992b; Boneka et al., 1998). Predatory fish may also be important predators of juvenile *Littoraria* and species from lower vertical levels (Hughes and Jones, 1985; Hughes and Mather, 1986; Borjesson and Szelistowski, 1989; Catesby and McKillup, 1998; Duncan and Szelistowski, 1998). In salt marshes both portunid crabs and predatory gastropods (*Melongena*) attack *L. irrorata* (Warren, 1985; West and Williams, 1986; Dix and Hamilton, 1993; Schindler et al., 1994). There is limited evidence of predation by birds on *Littoraria* species in the mangrove canopy (Reid, 1987; Cook and Garbett, 1992). An unusual predatory association has recently been reported in southern Queensland, where two species of sarcophagid flies are a significant cause of mortality in *L. filosa* (Sowerby, 1832) (McKillup and McKillup, 2000; McKillup et al., 2000; Pape et al., 2000). In Vietnam, South East Asia and India the larger *Littoraria* species are gathered locally for food by humans (Kasinathan and Shanmugam, 1988; Poutiers, 1998).

On tropical rocky shores *Littoraria* have been reported to graze on diatoms, microalgae, cyanobacteria and bacteria, but in mangrove and saltmarsh habitats additional sources of food are available. *Littoraria* species appear to be opportunistic grazers, ingesting a range of fungal, algal, detrital and plant material and their role in food webs has been examined (Kemp et al., 1990; Currin et al., 1995). Several investigators have stressed the likely importance of marine fungi in the diet of *Littoraria* inhabiting both mangrove trees (Kohlmeyer and Bebout, 1986; Christensen, 1998) and grass (Newell and Barlocher, 1993; Barlocher and Newell, 1994a, b; Graca et al., 2000). Whether mangrove plant tissue is a significant food source is debated (Ohgaki, 1990; Jensen, 2000; Lee, 2001) and the composition of the diet may depend upon vertical zonation and tree species (Jensen, 2000). The mechanical function of the radula has not been studied, but it has been shown that the form of the radular teeth differs consistently in specimens of the same species sampled from rock and wood substrates, implying that tooth shape is phenotypically plastic (Reid and Mak, 1999). Growth rates can be rapid in tropical *Littoraria* species, most reaching asymptotic size in six months to one year (Maruthamuthu and Kasinathan, 1985; Burgett et al., 1987; Cruz, 1989; Boneka et al., 1997; Jensen et al., 1999; Jensen, 2000). Breeding and population characteristics have been reported in several *Littoraria* species (Berry, 1986; Maruthamuthu and Kasinathan, 1986; Yi and Li, 1988; Herjanto and Thomas, 1995; Jensen et al., 1999).

The intraspecific variability of littorinid shells has been a common cause of taxonomic confusion in the past. In a morphometric study of *L. angulifera* throughout its Atlantic range, Merkt and Ellison (1998) reported strong intraspecific variation in shell shape, but argued that this was a consequence of ecophenotypic effects rather than genetic differentiation. However, an earlier study of the same species over a more restricted area had reached the opposite conclusion (Janson, 1985). When considering variation between species, it has often been observed that shell thickness decreases in species zoned at higher levels on the trees, reflecting adaptation to the severity of aquatic predation at lower levels (Cook et al., 1985; Borjesson and Szelistowski, 1989; Duncan and Szelistowski, 1998) and the danger of dislodgement in the canopy (McMahon, 1985).

In many *Littoraria* species the most striking aspect of shell variability is the color polymorphism of the shell. Indeed this feature has stimulated the most active field research on the genus, so that species of *Littoraria* have become recognised as a model system for the study of visible genetic polymorphism (Cook, 1992). Unfortunately, early studies suffered from the confusion of several different sympatric species (Hughes and Jones, 1985; Hughes and Mather, 1986). It has been observed that there is a consistent correlation between monomorphic (although still variable) shells and a low-level habitat on trunks and branches, whereas species inhabiting foliage are polymorphic (Cook, 1983, 1986b), although under exceptional circumstances polymorphism has also been reported in a trunk-dwelling species (Cook and Bridle, 1995). The three principal morphs are yellow, brown and pink (or 'orange') and each appears to be cryptic against different parts of the visually varied background of the mangrove canopy, or to mimic elements of the foliage (Cook, 1983; Reid, 1987). Assuming that the polymorphism is genetic in origin and not selectively neutral, there are a number of mechanisms by which it could be maintained by natural selection (Reid, 1987; Cook and Garbett, 1992). Evidence has accumulated for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significant changes in morph frequencies according to the composition of the background (e.g. tree species and abundance of foliage; Reid, 1987; Cook and Garbett, 1989; Cook, 1990a; Schmidt, 1998) and there has been one manipulative field experiment that suggested the operation of frequency-dependent (apostatic) selection (Reid, 1987). Nevertheless, the identity of possible visual predators is a matter of speculation; birds, crabs and even flies have been suggested (Reid, 1987; Cook and Garbett, 1992; McKillup et al., 2000). The differences in thermal properties of the morphs may result in behavioral differences that contribute to site selection and background matching (Cook, 1986b; Cook and Freeman, 1986; Reid, 1987). The color morphs of *L. pallescens* have also been shown to differ in shell strength, size, variance and growth rate (Cook et al., 1985; Cook, 1990b; Cook and Kenyon, 1993; Boneka, 1996; Boneka et al., 1997).

Relatively few new anatomical studies have been carried out since 1986. Egg capsule shape has been documented in a number of additional species (Berry, 1986; Ho, 1987; Mak, 1995). The flagellum-like structure of the paraspermatozoa is a character of phylogenetic significance (Reid, 1999b); this has been named the pseudotrich and has been the subject of structural and ontogenetic study (Healy and Jamieson, 1993; Buckland-Nicks et al., 2000). The functions of paraspermatozoa have been reviewed by Buckland-Nicks (1998; Buckland-Nicks et al., 1999). Eertman (1996) described the ultrastructure of the gill filaments of *L. articulata*.

MATERIAL AND METHODS

Shell dimensions were measured with vernier calipers to 0.1 mm. Shell height (H) is the maximum dimension parallel to the axis of coiling, shell breadth (B) the maximum dimension perpendicular to H, and the length of the aperture (LA) the greatest length from the junction of the outer lip with the penultimate whorl to the anterior lip. Shell shape was quantified as the ratio H/B and H/LA (relative spire height, SH).

For general accounts of the male and female anatomy of *Littoraria*, and methods of study, see Reid (1986a, 1999a). Living animals were relaxed in 7.5% magnesium chloride in fresh water, fixed in 10% seawater formalin and stored in 80% ethanol before examination. Paraspermatozoa were examined from the seminal vesicles of specimens fixed and stored in 10% seawater formalin. The relative radular length was the total radular length divided by shell height. Radulae were cleaned by soaking in a hypochlorite bleaching solution at room temperature for about 5 min, rinsed in distilled water, mounted on a film of polyvinyl acetate glue on glass, allowed to dry in air, and coated with gold and palladium before examination in a scanning electron microscope. Unworn portions of radulae were viewed in three orientations: in standard flat view (from vertically above the radula, to show shapes of teeth), at an angle of 45° from the front end of the radula (to show shapes of tooth cusps), and at an angle of 45° from the side of the radula (to show relief).

Institutional abbreviations:

AMS: Australian Museum, Sydney
ANSP: Academy of Natural Sciences of Philadelphia
BMNH: Natural History Museum, London
MNHN: Muséum National d'Histoire Naturelle, Paris
NSMT: National Science Museum, Tokyo
NMW: National Museums and Galleries of Wales, Cardiff
RNHL: Nationaal Natuurhistorisch Museum, Leiden
USNM: National Museum of Natural History, Smithsonian Institution, Washington, D.C.
ZMA: Institute of Taxonomic Zoology, University of Amsterdam

SYSTEMATICS

Littoraria (Littorinopsis) scabra (Linnaeus, 1758)

Distribution: New records: Mascarene Islands: Rodrigues (NMW). Vietnam: Lo River, Nha Trang (BMNH). China: Sanya, Hainan Island (BMNH). Taiwan: Tan Shui (BMNH). Japan: Amami O Shima (Kyushu University), Inoda, Ishigaki Shima (BMNH), Chichijima and Hahajima, Ogasawara Islands (Fukuda, 1993).

Littoraria (Littorinopsis) lutea (Philippi, 1847)

Distribution: New records: Vietnam: Lo River, Nha Trang (BMNH). Indonesia: Lembar, Lombok (BMNH).

Littoraria (Littorinopsis) pallescens (Philippi, 1846)

Distribution: New records: Vietnam: Lo River, Nha Trang (BMNH). China: Sanya, Hainan Island (BMNH). Taiwan: Tan Shui (BMNH). Japan: Naze, Amamioshima (Kyushu University), Kabira Bay, Ishigaki (BMNH).

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Figures 1–13. Shells of *Littoraria bengalensis* new species and *Littoraria intermedia*. **1–11.** *L. bengalensis*. **1, 7.** Batu Maung, Penang, Malaysia (BMNH 20010115; **1,** male; **7,** female). **2, 4, 8.** Paratypes, Hare Island, Gulf of Mannar, Tamilnadu, India (BMNH 20010140; **2, 8,** female; **4,** male). **3, 6.** Tuticorin, Tamilnadu, India (BMNH 20000783, females). **5.** Sungei Merbok, near Pantai Merdeka, Kedah, Malaysia (BMNH 20010118, male). **9.** Ao Nam Bor, Phuket Island, Thailand (BMNH 20010117, female). **10.** Holotype: Hare Island, Gulf of Mannar, Tamilnadu, India (BMNH 20010114, male). **11.** Ao Nam Bor, Phuket Island, Thailand (BMNH 20010116, male). **12, 13.** *L. intermedia*, Hare Island, Gulf of Mannar, Tamilnadu, India (BMNH 20000754; **12,** male; **13,** female).

Western Australia: Berkeley River, W coast Joseph Bonaparte Gulf (BMNH); Mangrove Bay, Cape Range (BMNH). Mariana Islands: Merizo, Guam (BMNH).

Littoraria (*Littorinopsis*) *bengalensis* new species
(Figures 1–11, 14–16, 20–22, 34, 35)

Littorina scabra—Nielsen, 1976: 1–4, fig. 1A (in part, includes *L. scabra* (Linnaeus, 1758), *L. pallescens* (Philippi, 1846) and probably *L. intermedia* (Philippi, 1846)).
Littoraria intermedia—Reid, 1985: 39–68, figs 9, 11 (zonation) (fig. 9 includes *L. intermedia* (Philippi, 1846)). Cook and Garbett, 1989: 5, fig. 1e, 2e (penis) (in part, includes *L. intermedia* (Philippi, 1846)).
Littoraria (*Littorinopsis*) *intermedia*—Reid, 1986a: 124–135, figs 43b, 44e, f, 45c, d, 46b (penis), 46k (paraspermatozoa) (in part, includes *L. intermedia* (Philippi, 1846)).

Etymology: From the Bay of Bengal, of which the known distributional range of this species spans the southern part.

Types: Holotype BMNH 20010114 (Figure 10); 17 dry paratypes BMNH 20010140 (Figures 2, 4, 8); 100 paratypes in ethanol BMNH 20000755; 4 dry paratypes USNM 1000887.

Type locality: Hare Island, Gulf of Mannar, Tamilnadu, India.

Material Examined: 32 lots; 15 penes; 7 sperm samples; 4 pallial oviducts; 4 radulae.

Shell (Figures 1–11): Adult size range 12.3–28.6 mm. Shape elongate-turbinate (H/B = 1.49–1.86; SH = 1.72–2.16); whorls moderately rounded, suture impressed, periphery of last whorl angled, often with a raised rib; relatively thin-shelled. Mature lip sometimes slightly flared in males, varices rarely formed. Columella wide, pillar straight or slightly convex, excavated. Sculpture of (8)9–10 primary spiral grooves on spire whorls, equally spaced; primary grooves remain as incised lines or up to 0.2–0.3 rib width on last whorl, often slightly deeper and wider posteriorly (where occasionally posterior groove may be 0.5–1 rib width); intervening ribs remain undivided until last whorl, where 2–4 posterior ribs (excluding rib adjacent to suture) become divided by a central impressed line; peripheral rib usually raised, occasionally carinate; sometimes a narrow riblet interpolated in 2–3 posterior grooves; basal ribs finer; total ribs on last whorl 21–35. Surface glossy, spiral microstriae faint or absent. Protoconch 0.35 mm diameter, 3.5 whorls, with spiral ribs and sinusigera notch. Color variable: ground color cream, pale yellow or ochre; pattern of dark brown dashes on ribs; on spire whorls dashes are usually axially aligned to form oblique or zigzag stripes, but on last whorl dashes become less discrete and break up into diffuse blackish to red-brown mottling; often a broad paler zone on middle of base; pattern sometimes faint, so that shell appears yellow with grey-brown mottling. Columella purple brown to dark violet; aperture with exterior pattern showing through and not obscured by the thin whitish callus.

Animal: Headfoot, operculum, pallial oviduct and radula (Figures 34, 35) do not differ significantly from those of *L. intermedia* as described by Reid (1986a). Penis (Figures 14–16, 20) bifurcate; large dark brown glandular disc carried on long branch of base; smooth blade-shaped filament with mucronate tip, separated from wrinkled base by constriction, 0.4–0.5 total length of penis; entire vas deferens from tip of penial filament to prostate closed as a duct. Paraspermatozoa (Figure 21; Reid, 1986a: fig 46k) 14–26 µm (including rod pieces); rod pieces composed of a bundle of several narrow elements, or rarely single, usually projecting from cell; cell filled with large round granules. Ovoviviparous; embryos brooded between gill folds in mantle cavity until veliger stage; development planktotrophic.

Distribution: Habitat on branches and foliage of mangroves (*Avicennia, Rhizophora, Sonneratia*) and maritime trees (*Pemphis*), up to 3.5 m above ground, always above water level; most frequent at seaward edge of mangrove forests, but extending far back into forest (see Reid, 1985: figs 9, 11, for zonation; as *L. intermedia*); only rarely found on rocks. Found in moderately turbid and estuarine localities as well as on nearshore islands. Range (Figure 22) from India to western Malay Peninsula and northern Sumatra. Records: India: Chaupati Beach, Mumbai (USNM); Vengurla (USNM); Mandovi Estuary, Goa (BMNH); Netravata R., Mangalore (USNM); Cochin Harbor (ANSP); Alleppey (BMNH); Tuticorin (BMNH, USNM); Krusadai I., Gulf of Mannar (BMNH); Portonovo, Tamilnadu (BMNH); Chennai (BMNH); Port Blair, Andaman Is (BMNH). Burma: Thayawthadangyi Kyun (Elphinstone I.), Mergui Arch. (BMNH); Kadan Kyun (King I.), Mergui Arch. (BMNH); Lanbi Kyun (Sullivan I.), Mergui Arch. (BMNH). Thailand: Goh Contee, Ranong (MCZ); 70 km S Ranong (BMNH); Ao Nam Bor, Phuket I. (BMNH); Pulau Tanga, Butang Is (USNM). Malaysia: Merbok Estuary (BMNH); Batu Maung, Penang (BMNH); Matang Estuary (BMNH). Indonesia: Belawan, Deli, Sumatra (RNHL); Sinabang, Simeulnë I. (RNHL).

Remarks: In his discussion of *L. intermedia* Reid (1986a: 134) noted that specimens from southwestern Thailand, Penang and India had thin-walled, often large shells with an irregular color pattern. This form occurred together with typical *L. intermedia* at Phuket Island, Thailand, yet was not considered distinct, since it was claimed that intermediates were present and because no anatomical differences were observed. Although the shells can be closely similar and anatomical differences are slight, new evidence supports recognition of this form as a distinct species. This was first suggested by field observations at the type locality (Hare Island, Gulf of Mannar). Here, three species occurred together on shrubs of *Pemphis* overhanging a sheltered sandy lagoon behind a fringing reef. There was a clear zonation: *L. intermedia* was present on trunks at a level of 0–30 cm above the high water mark; *L. scabra* occupied a zone 30–60 cm above high water, on trunks and branches,

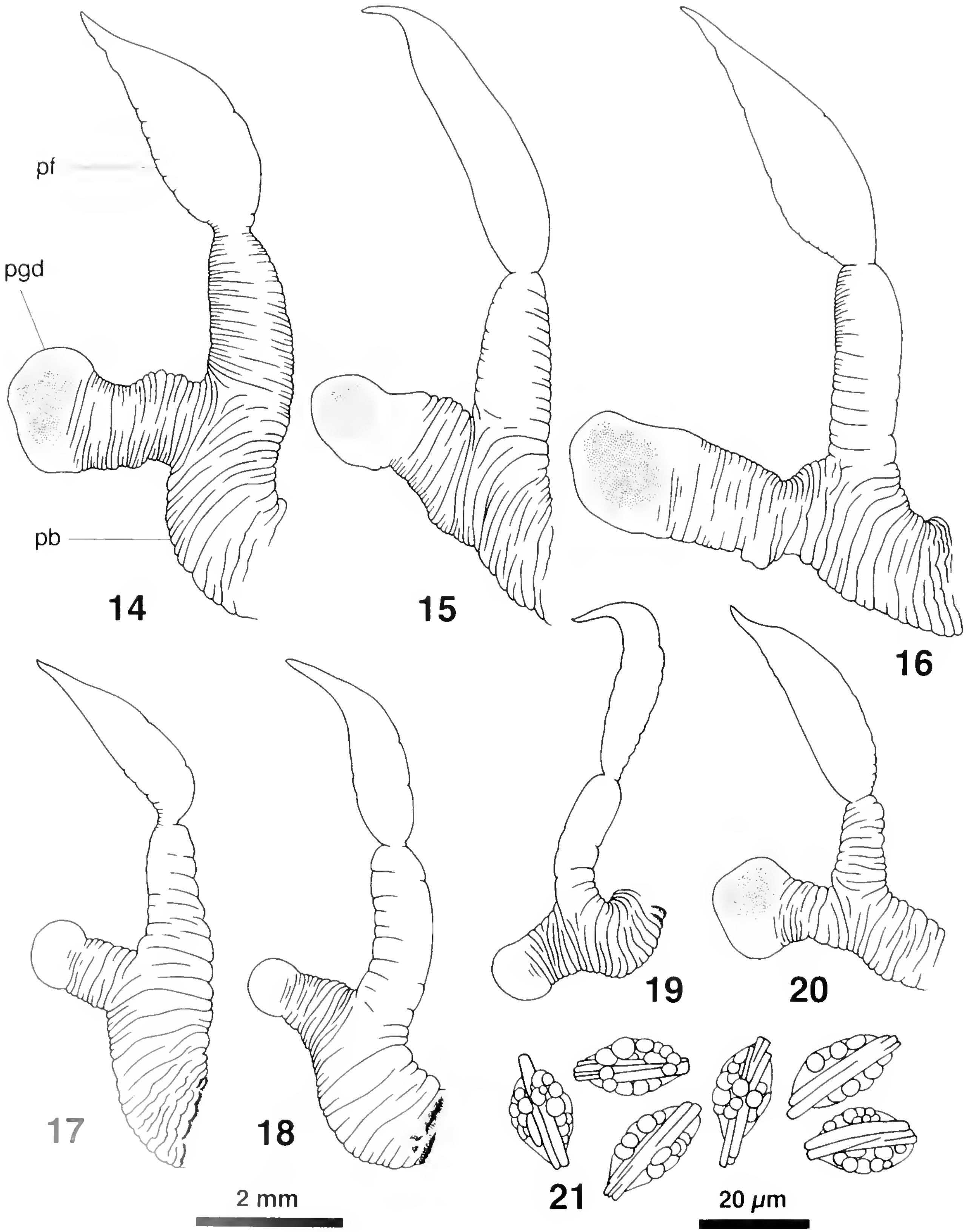
whereas a third species (*L. bengalensis*) occurred on both foliage and branches from a height of 30–100 cm. The three species could be separated by shell characters (see below) and, most significantly, all three were copulating only with conspecifics. Subsequent anatomical examination found a consistent difference in the penis of *L. bengalensis* and *L. intermedia*. Reexamination of museum collections has revealed sympatric occurrence (mixed samples) of *L. bengalensis* and *L. intermedia* at the following additional localities: Galle, Sri Lanka (BMNH); two islands in Mergui Archipelago, Burma (BMNH); Ao Nam Bor, Phuket I., Thailand (BMNH); Pulau Tanga, Butang Is, Thailand (USNM); Sinabang, Simeulue I., Indonesia (RNHL). In each case separation of shells was straightforward, with no intermediates, and males from Ao Nam Bor were also distinguished using the same penial characters as at the type locality.

The differences between *L. bengalensis* and *L. intermedia* are summarised in Table 1. The shells of *L. intermedia* show considerable geographical and ecotypic variation (see Reid, 1986a, and below), so the descriptions apply only to specimens from within the geographical distribution of *L. bengalensis* and from the mangrove habitat. For comparison, shells of *L. intermedia* from the type locality of *L. bengalensis* are illustrated (Figures 12, 13). The shells of *L. bengalensis* are usually larger, up to 28.6 mm, those of *L. intermedia* rarely exceeding 18 mm (although the maximum size of the species as a whole is actually greater, 32 mm; Reid, 1986a). They are also of thinner texture, with more sharply angled periphery, than those of *L. intermedia*. Sexual dimorphism is evident in both species (Figures 1–13), males being smaller and with a relatively lower spire and larger aperture (Reid, 1986a); however, males of *L. bengalensis* often have a more elongately patulous shape, reminiscent of a *Succinea* (compare Figures 5 and 12). The overall color of the shell is ochraceous or yellowish, with brown pattern, in *L. bengalensis*; in contrast, that of *L. intermedia* is grey with black to brown pattern. In detail, the dark pattern of dashes on the ribs is similar on the early whorls of both species, but on the final whorl the dashes of *L. intermedia* remain more discrete and axially aligned, whereas in *L. bengalensis* the pattern becomes more diffuse and mottled. In both species there appears to be a direct effect of substrate upon shell color, presumably mediated through diet (Reid, 1986a). Shells from *Rhizophora* and *Pemphis* are darkly patterned, whereas those from *Avicennia* and *Sonneratia* are conspicuously paler. Only *L. intermedia* is known to occur on rocks and these too are usually relatively pale in color.

The only anatomical difference that has been observed is the shape of the penis: that of *L. bengalensis* has a more robust filament and a larger glandular disc borne on a longer branch of the base (although the proportions of the penis depend upon the degree of relaxation, see Reid, 1986a: fig. 46). In all animals examined the penial glandular disc of *L. bengalensis* was dark brown, whereas that of *L. intermedia* was cream or yellowish. There may also be a difference in the paraspermatozoa: in *L. bengalensis* the rod pieces usually project (Figure 21; Reid, 1986a: fig. 46k), but in *L. intermedia* they seldom pierce the oval outline of the cell (Reid, 1986a: figs 46i, j) (based on 7 and 5 samples respectively).

There is little information on the comparative habitats of *L. bengalensis* and *L. intermedia* since the two have only recently been distinguished in the field and found in sympatry. The available observations indicate that *L. bengalensis* is found higher on the trees, throughout a greater width of the mangrove forest and that it is more tolerant of turbid and estuarine conditions. For example, at the muddy bay of Ao Nam Bor, Phuket Island, Reid (1985: fig. 9) recorded *L.* '*intermedia*' from throughout a mangrove stand 80 m wide, through to the landward zone and at heights of up to 3.5 m above the ground. Both species are present at this site (collections of Reid in BMNH) and since in other parts of its range *L. intermedia sensu stricto* is known to occur mainly at the seaward edge and at low levels on trees, it is likely that the high-level and landward records apply to *L. bengalensis*. At the muddy, turbid site of Batu Maung, Penang, only *L. bengalensis* was present and here Reid (1985: fig. 11, as *L. intermedia*) recorded it from throughout a belt of *Avicennia* 10 m wide and from up to 2.0 m above the ground. Likewise in the nearby Merbok Estuary *L. bengalensis* occurred alone and from seaward edge to landward fringe (personal observation). The type locality of *L. bengalensis* is a sandy island with a fringing reef and clear water; here both species occurred and *L. bengalensis* was found above the level of *L. intermedia* and on both foliage and branches, whereas the latter was present only on trunks (and has rarely been found on leaves elsewhere; Reid, 1985). *Littoraria bengalensis* has so far been recorded almost exclusively on trees (one specimen on a sheltered rocky shore near Ranong, Thailand; BMNH), whereas *L. intermedia* is commonly found on both trunks and sheltered rocky shores (Reid, 1985, 1986a).

Reid (1986a: 57–58) discussed a distinction between *Littoraria* species with 'oceanic' and 'continental' distribution patterns, representing extremes on a gradient of ecological tolerance. The former referred to a suite of habitat characteristics including clear water, normal salinity, narrow mangrove fringes (or seaward edges of broad mangrove belts) and offshore islands. In contrast 'continental' habitats were characterised by turbid, estuarine water, eutrophic conditions, and broad forests on continental margins. It is clear that on this continuum *L. bengalensis* extends to more 'continental' habitats than *L. intermedia*. For example, in the Andaman Sea both species have been recorded from the Andaman Islands, Mergui Archipelago, Phuket Island and Butang Islands (details given above); these are all 'oceanic' sites. However, at a muddy site on Penang and in both the Merbok and Matang Estuaries, and in the vicinity of Ranong, on or close to the mainland of the Malay Peninsula, *L. bengalensis* occurred alone (large collections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by D.G. Reid, E. Ashton and J.D. Taylor respectively, all BMNH). Similarly, in India *L. bengalensis* has been recorded over a large extent of the continental coastline, from Mumbai to Chennai, from islands in the Gulf of Mannar and from Galle in Sri Lanka. In contrast, in the same region *L. intermedia* has been recorded only from islands in the Gulf of Mannar, from Galle and from Trincomalee, Sri Lanka (see below), all of which appear to be 'oceanic' sites. On a wider geographical scale the distribution of *L. intermedia* extends across the Pacific to the islands of Hawaii and Polynesia, again reflecting the 'oceanic' character of this species.

The northern limits of *L. bengalensis* in the Bay of Bengal are not clear, owing to the few available collections from northeastern India and Bangladesh. So far, only two *Littoraria* species have been recorded from Bengal and Bangladesh, *L. delicatula* and *L. melanostoma* (Reid, 1986a; see below).

The many morphological similarities between *L. bengalensis* and *L. intermedia* leave little doubt that the two are sister species. Likely synapomorphies include the blade-shaped penial filament with mucronate tip and the bundles of narrow rod-pieces in the paraspermatozoa, both unique in the genus. The closed penial vas deferens is a likely synapomorphy of a clade comprising *L. bengalensis*, *L. intermedia*, *L. subvittata* Reid, 1986 and *L. philippiana* (Reeve, 1857) (Reid, 1999b).

Confusion of *L. bengalensis* with other species is less likely. In southern India and the southern Andaman Sea its range overlaps with that of *L. scabra* and the two can be found sympatrically in relatively 'oceanic' habitats (including the type locality in the Gulf of Mannar). *Littoraria scabra* is easily recognised by its wide, white columella. *Littoraria pallescens* (Philippi, 1846) is even more oceanic in character than *L. scabra* and has been recorded sympatrically with *L. bengalensis* only in the Andaman Islands, Penang, Butang Islands and Phuket Island; it is distinguished by its colorful, polymorphic shell, lack of secondary sculpture and the rounded inner lip of the aperture. In each case penial characters are diagnostic (Reid, 1986a). The distribution of *L. bengalensis* just touches that of *L. delicatula*, single specimens of the latter having been seen from the Gulf of Mannar and the Andaman Islands, although most are from the head of the Bay of Bengal (see below). Shells of these two species can be superficially similar (both may be thin-shelled, and yellow with a faint or diffuse pattern). Nevertheless, they can always be distinguished by the more numerous primary grooves (11–14) and much finer sculpture (35–50 ribs on final whorl) of *L. delicatula*; the columella of that species is narrow and excavated in the typically very delicate shells, although it may approach that of *L. bengalensis* in width in occasional thicker shells. The shape of *L. delicatula* is subtly different: the spire whorls are flatter and the spire usually slightly taller. Most importantly, the penis of *L. delicatula* is entirely different (Figures 31, 32, see below).

Littoraria (Littorinopsis) intermedia (Philippi, 1846)
(Figures 12, 13, 17–19, 22)

Synonymy as in Reid (1986a) excluding the entries now listed under *L. bengalensis* above. New references:

Littoraria (Littorinopsis) intermedia.—Reid 1986a: 124–135, figs 43a, c–i, 44a–d, g–i, 45a, 45b (protoconch), c, 45f (radula), 46a, c–h (penis), 46i, j (paraspermatozoa), 46l–o (oviduct), 47 (distribution) (in part includes *L. bengalensis* new species).

Distribution: Records and distribution as in Reid (1986a: 132–134, fig. 47), but excluding all records from mainland India except those listed below, and also excluding records from Penang, Merbok estuary and Belawan (the excluded records apply to *L. bengalensis*, see above). The doubtful record from the Galápagos Islands (Reid, 1986a: 134) is now considered unreliable and should be excluded (Reid and Kaiser, 2001). New and reconfirmed records: Kenya: Kilifi R. estuary (BMNH). Saudi Arabia: Jeddah (BMNH). Oman: Masirah I. (ZMA); Khor Al-Jarama, Ras Al-Hadd (BMNH); Bandar Khayran (BMNH). United Arab Emirates: Fujaira (BMNH); Ras Al-Khaimah Khor, Dubai (BMNH); Khor Kalba, Sharjah (BMNH). India: islands in Cochin Harbour, Kerala (ANSP); Manali I. and Hare I., Gulf of Mannar (BMNH). Thailand: Krabi (BMNH). Malaysia: Pulau Gaya, Kota Kinabalu, Sabah (BMNH); Kudat, Sabah (BMNH). Vietnam: Lo R., Nha Trang (BMNH). China: Beigang I., Hainan (BMNH). Indonesia: Kuta Beach, Lombok (BMNH). Philippines: Mandalee, S El Nido, N Palawan (BMNH). Taiwan: Tan Shui (BMNH). Japan: Ishigaki (BMNH); Yakushima (S. Kozumi Colln); Amamioshima (S. Kozumi Colln); Shirahama, Wakayama (BMNH); Chichijima, Ogasawara Islands (Fukuda, 1993). Australia: Wooli Wooli R., New South Wales (AMS). Tonga: Sopu, Nuku'alofa, Tongatapu (BMNH).

Remarks: Reid (1986a) characterised this as a typi-

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Figures 14–21. Penes and paraspermatozoa of *Littoraria bengalensis* new species and *Littoraria intermedia*. **14–16, 20.** Penes of *L. bengalensis*. **14–16.** Paratypes, Hare Island, Gulf of Mannar, Tamilnadu, India (BMNH 20000755; shell H = 17.0 mm, 16.1 mm, 16.6 mm). **20.** Ao Nam Bor, Phuket Island, Thailand (BMNH 20010116; shell H = 13.0 mm). **17–19.** Penes of *L. intermedia*. **17, 18.** Hare Island, Gulf of Mannar, Tamilnadu, India (BMNH 20000754; shell H = 12.8 mm, 15.3 mm). **19.** Ao Nam Bor, Phuket Island, Thailand (BMNH 20010119; shell H = 13.4 mm). **21.** Paraspermatozoa from one paratype of *L. bengalensis* (Hare Island, Gulf of Mannar, Tamilnadu, India, BMNH 20000755). Abbreviations: pb, penial base (wrinkled); pf, penial filament (smooth); pgd, penial glandular disc. Stipple on penial glandular disc indicates dark brown coloration; shading at base of penis indicates black pigment in epithelium.

Table 1. Summary of differences between *Littoraria bengalensis* new species and *L. intermedia* (shell characters apply to specimens from mangrove habitats in northeastern Indian Ocean only).

Character	*Littoraria bengalensis*	*Littoraria intermedia*
Shell shape	Larger (to 29 mm), thinner texture, peripheral angulation with raised rib	Smaller (to 18 mm), more solid, more rounded periphery
Shell color	Ochre to yellow, with brown pattern; on last whorl the dark dashes are diffuse	Grey, with black to brown pattern; on last whorl the dark dashes remain discrete and axially aligned
Penis	Robust filament, brown glandular disc borne on long branch of base	More slender filament; cream glandular disc borne on shorter branch of base
Paraspermatozoa	Rod pieces project from cell	Rod pieces seldom project from cell
Habitat	More tolerant of turbid and estuarine conditions; occurs higher on trees and throughout forest; found on trunks, branches and foliage, rarely on rocks	Preference for clear water, found lower on trees and only common at seaward edge of forest, found on roots, trunks and sheltered rocks
Distribution	Northeastern Indian Ocean, from India to western Malay Peninsula and northern Sumatra	Occurs widely throughout Indo-West Pacific region

cally oceanic species, with a wide distribution from South Africa to the Red Sea, throughout the Indo-West Pacific tropics to Hawaii and Polynesia. Within this area he pointed out three distinctive geographical forms, from the central Pacific, from the western Indian Ocean (including the Red Sea) and from India and the Andaman Sea. It is demonstrated above that the last of these is a distinct species, *L. bengalensis*. Its recognition removes the anomaly of the occurrence of this 'form' in the relatively continental conditions of broad mangrove forests in estuaries on the mainland shores of the western Malay Peninsula. An obvious question is whether the other 'forms' might also deserve specific status. Accordingly, much new anatomical material has been examined

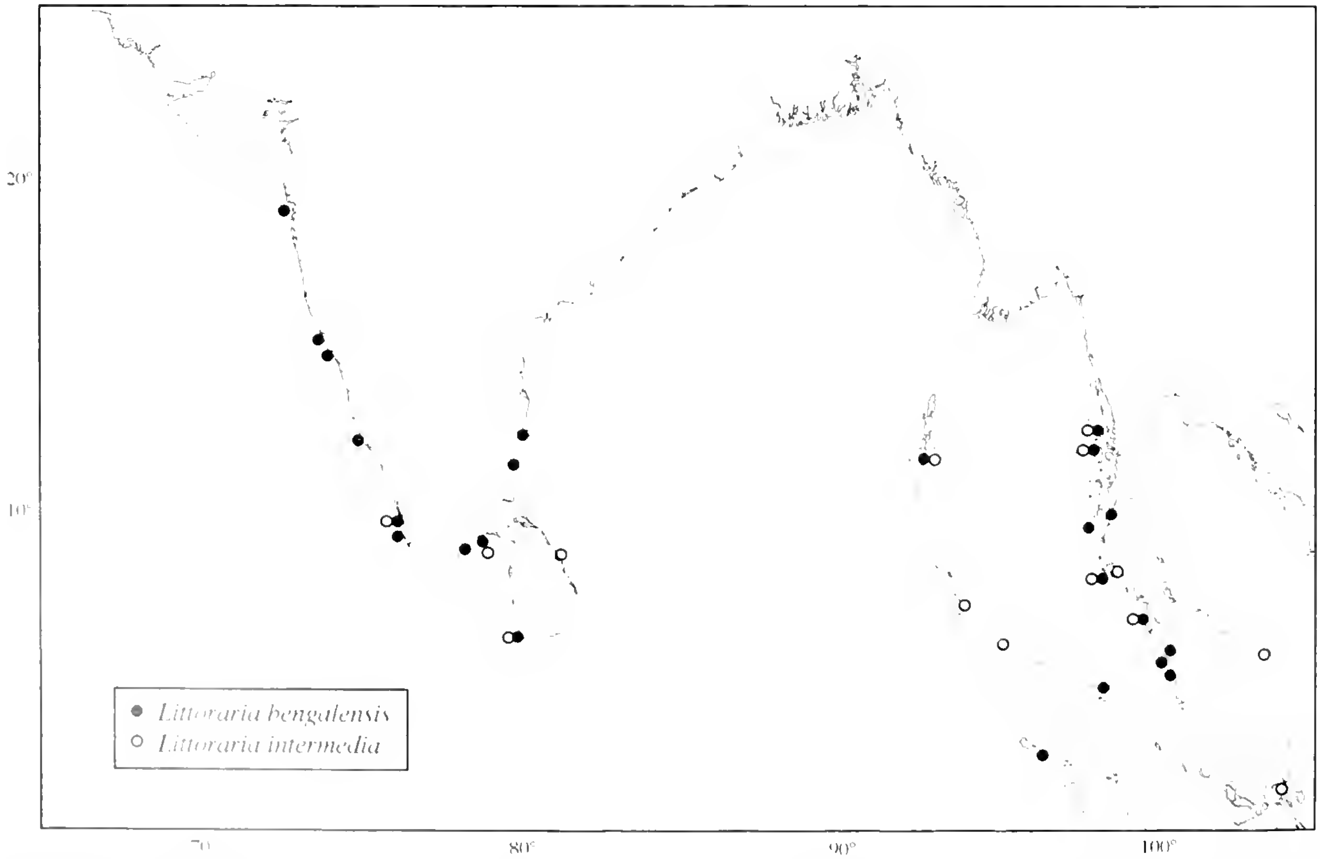


Figure 22. Geographical distribution of *Littoraria bengalensis* with (for comparison) the records of *Littoraria intermedia* from the same area (see text for lists of records).

from throughout the range of this species (in particular 66 penes have been drawn). However, no obvious discontinuities have been found. Furthermore, in areas such as the Solomon Islands, New Caledonia and Fiji, where overlap in the ranges of a putative Indo-Malay species (the 'typical form') and a putative central Pacific species might have been predicted, no evidence has been found for the sympatric occurrence of discrete conchological or anatomical types. Instead, the evidence continues to suggest a single widespread species, typical of oceanic habitats, in which shell characters show small and gradual changes (in the color pattern, frequency of color morphs, and presence of secondary sculpture) across the considerable geographical range. Shell characters continue to show a strong correlation with habitat as well as geography, as pointed out by Reid (1986a). Thus, throughout the range, those specimens from rocky shores (and from certain mangrove tree species such as *Avicennia* and *Sonneratia*) are paler in color and show a more diffuse pattern, in comparison with the typically dark shells found on *Rhizophora* trees, which are the prevalent shell type in the Indo-Malay and Australian regions.

The new records listed above significantly extend the known range of this species in Arabia, the South China Sea, and southeastern Australia. In Japan, the record from Shirahama confirms the (presumably sporadic) occurrence of this species in the Kii Peninsula (the record in Reid, 1986a, was based on a shell illustrated by Habe, 1964). Additional collecting in northwestern Australia (M. Stuckey, personal communication) has failed to find this species further west than the Coburg Peninsula, so its absence from Western Australia appears to be real.

Littoraria (Littorinopsis) subvittata Reid, 1986a

Distribution: New record: Mascarene Islands, Rodrigues (NMW).

Littoraria (Littorinopsis) philippiana (Reeve, 1857)

Distribution: New records: New South Wales, Wooli Wooli River (AMS).

Littoraria (Littorinopsis) filosa (Sowerby, 1832)
(Figures 23–30)

Animal: Penis (Figures 23–30): in specimens from Western Australia the glandular limb is often longer and more robust than previously reported (Reid, 1986a, fig. 54); it may be as long and up to 3 times as broad as the penial filament.

Distribution: New records: Northern Territory, Forsyth Creek, E coast Joseph Bonaparte Gulf (BMNH). Western Australia: Berkeley River and Revely Island, W coast Joseph Bonaparte Gulf (BMNH).

Remarks: Reid (1986a) noted that the geographical form found from Cape Leveque to Exmouth Gulf in Western Australia differed from the typical form on the east and north coast of Australia by more numerous but less prominent primary ribs and by details of color pattern. Taxonomic recognition was not considered justified since no anatomical differences were detected. New material from throughout the range in Western Australia (including the two listed above that fill in a gap in the known distribution) confirms the reported shell differences, but adds some significant details. The typical carinate (eastern) shell type extends to both localities in Joseph Bonaparte Gulf listed above, whereas a large sample (about 100, BMNH) from Cape Leveque displays characteristics intermediate between eastern and western shells. The western forms often (but not always) have penes with an unusually long and robust glandular branch of the base, exceeding in size any seen from northern or eastern Australia (samples of 30 western and 55 eastern penes). In none of the samples from Western Australia or Northern Territory is there any morphological evidence for a mixture of two discrete shell types with correlated penial differences. The earlier taxonomic conclusion therefore seems justified from a morphological viewpoint, and the evidence appears to show a blending of characters between two forms with a continuous distribution, rather than allopatry or limited overlap between two distinct forms. However, this interesting case should be investigated with genetic techniques (presently being done by M. Stuckey, University of Western Australia).

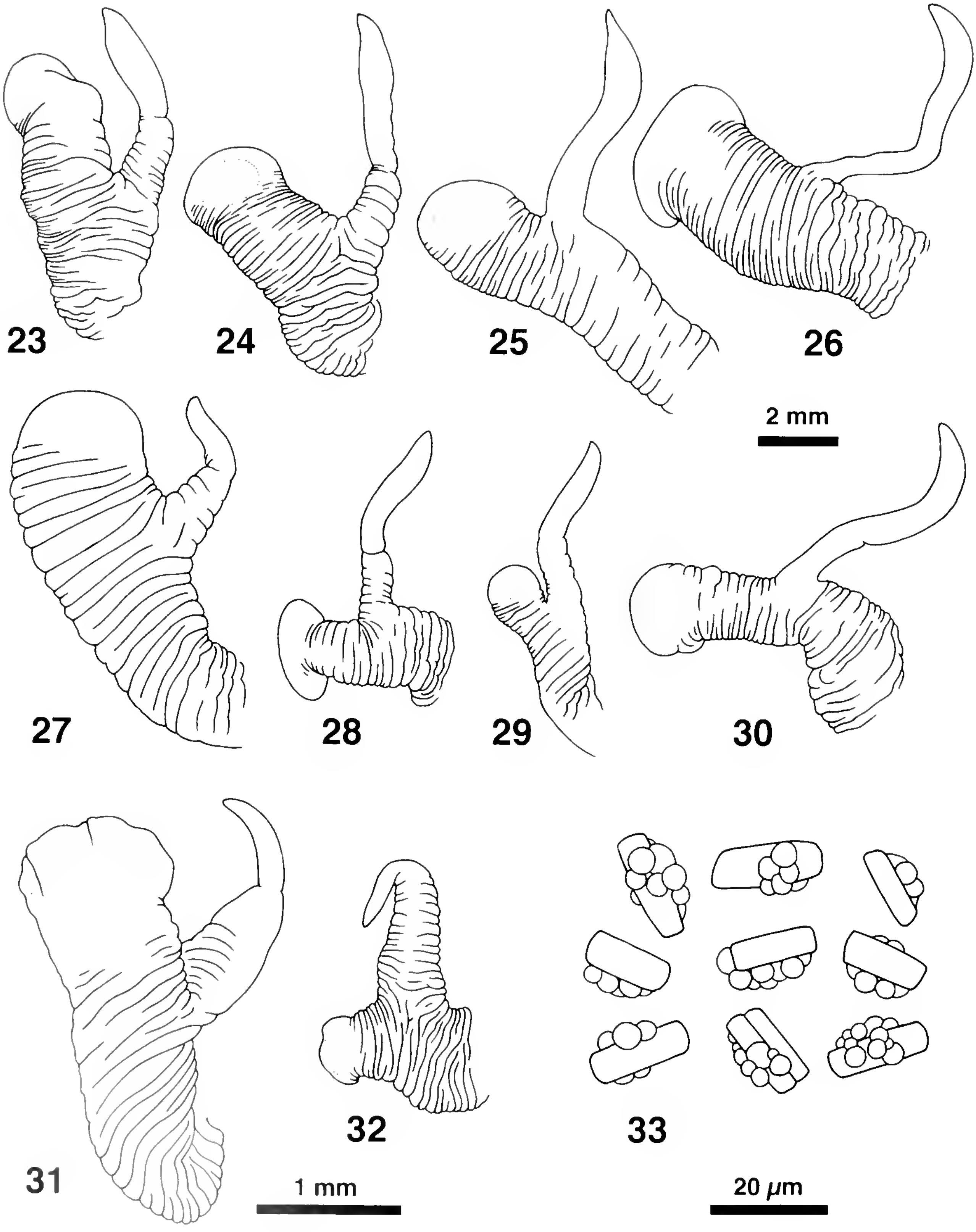
The apparent trend towards a longer glandular branch in the penis of the western form of *L. filosa* might repay further investigation. It could be significant that the eastern form (with relatively shorter glandular branch) is broadly sympatric with *L. philippiana*, a congener with a much longer glandular branch. In contrast the western form (with relatively longer branch) is largely sympatric with *L. cingulata*, in which penial shape is more similar to that of the eastern form of *L. filosa* (see Reid, 1986a: figs 41, 58). If penial shape is a species recognition character, its variation within *L. filosa* might suggest a case of character displacement.

Littoraria (Littorinopsis) ardouiniana (Heude, 1885)

Distribution: New records: Taiwan, Tan Shui; China, Sanya, Hainan; Vietnam, Sun Sot Cave, Ha Long Bay, Lo River, Nha Trang; Singapore, Changi South (all BMNH).

Littoraria (Littorinopsis) delicatula (Nevill, 1885)
(Figures 31–33, 36, 37)

Animal: Penis (Figures 31, 32): bifurcate; glandular disc large, with thin margin; filament small, 0.2 total length of base, separated from wrinkled base by constriction; sperm groove open. Paraspermatozoa (Figure 33): 14–20 µm, oval, 1 (rarely 2) large rectangular rod piece filling cell; granules large, few, distinct (observation of single sperm sample preserved in 80% ethanol,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1 mm
20 μm

which may cause shrinkage of about 20% (Reid, 1996: 6). No data on female. Radula (Figures 36, 37): relative length 0.76; rachidian tooth: base flared, central cusp shield-shaped, small cusp and one denticle on each side; lateral tooth: 5 cusps, largest central cusp blunt; inner marginal tooth: 4 cusps; outer marginal tooth: 5 cusps.

Distribution: Habitat: foliage of *Avicennia alba* on muddy river bank; water of low salinity (from 2–3% in wet season to 16.8% in dry season) (G. Pendred, personal communication). New records: Bodra Kaal, Chavlabogi, Sundarbans, Bangladesh (BMNH); Krusadai Island, Gulf of Mannar, India (BMNH).

Remarks: Reid (1986a) did not have access to any preserved specimens, but since then two males have been dissected and one radula prepared. Based on some similarity of shells, Reid (1986a) suggested that *L. delicatula* was most closely related to *L. ardouiniana* and that anatomical evidence was required to confirm that they were indeed distinct. The newly described penial form is sufficiently different from that of *L. ardouiniana*, in which the filament is large (up to half total length of penis; Reid, 1986a) to leave no doubt that the two are separate species. The paraspermatozoa are similar in both. The penis of *L. delicatula* does not differ significantly from that of *L. pallescens* and the radulae of these species are also closely similar. Radular tooth form is not, however, a reliable taxonomic character in *Littoraria* (Reid and Mak, 1999). Despite the penial similarity *L. delicatula* is believed to be distinct from *L. pallescens*, since the shells are very different (delicate, with 11–14 primary grooves, 35–50 ribs on last whorl and narrow columella in *L. delicatula*; solid, with 9–10 primary grooves, no secondary sculpture and broad columella in *L. pallescens*; see Reid, 1986a). Paraspermatozoa also differ, being rounded with small rod pieces in *L. pallescens* (although only a single sample has been seen in *L. delicatula*). These two have not yet been collected together, but both have been recorded from the Andaman Islands (Reid, 1986a), so that the conclusion that they are distinct might be tested in future. There is a superficial similarity to *L. bengalensis* (see above).

The new record from the Gulf of Mannar greatly increases the known range of this species, previously recorded only from Port Canning (Bengal) and the Andaman Islands. It is likely, however, that the center of distribution is the northern Bay of Bengal. Only single shells are available from the Andaman Islands (BMNH; Reid, 1986a) and the Gulf of Mannar. The latter was collected in 1934 by R. Winckworth; the species was not found on a recent visit to the Gulf of Mannar (personal observation, 2000) and is presumably rare in this area.

Littoraria (Palustorina) melanostoma (Gray, 1839)

Distribution: New records: Japan: Miyako Island, Yaeyama Islands (Higo et al., 1999).

Remarks: Reid (1986a) recorded the rare occurrence of a pinkish orange morph in this normally monomorphic species. This has now been seen in two samples from localities in Ha Long Bay, Vietnam (BMNH); the frequency was low (2% and 5%, N = 24 and 41) and in each case the specimens were collected among saltmarsh grass (see Remarks on *L. carinifera*).

Littoraria (Palustorina) carinifera (Menke, 1830)

Shell: Two cases of color polymorphism have been recorded in this species, hitherto thought to be rather constant in coloration (Reid, 1986a). In a sample of 78 shells from Lembar, Lombok (BMNH), most had a cream to grey ground color with red brown pattern, but in seven shells (9%) the ground color was orange. The sample was collected on trunks of dwarf *Avicennia* and *Sonneratia* trees 1 m in height on a muddy foreshore. A second polymorphic sample was collected among saltmarsh grass 70 km south of Ranong, Thailand (BMNH). Here the shells were of the small, smooth form (e.g. Reid, 1986a: fig. 82f); the range of colors was similar and three (6.5%) of 46 shells were orange.

Distribution: New record: Indonesia: Lembar, Lombok (BMNH).

Remarks: Elsewhere in the subgenus *Palustorina* pinkish orange shells are very rarely encountered in *L. articulata* and *L. melanostoma*, although this morph is widely distributed (though always at low frequency) in polymorphic members of the subgenus *Littorinopsis*. *Littoraria carinifera* is normally found on trunks at low levels (up to 0.5 m) on trees in the landward fringes of mangrove forests (Reid, 1986a: 192) and shells from this habitat are of overall dark brown color and not polymorphic or variable. It may be significant that both polymorphic samples are from foliage in open sunny conditions, in other words from visually varied microhabitats where the animals might be exposed to visual predation (e.g. by birds or crabs). It is under exactly these conditions that the polymorphic species of the subgenus *Lit-*

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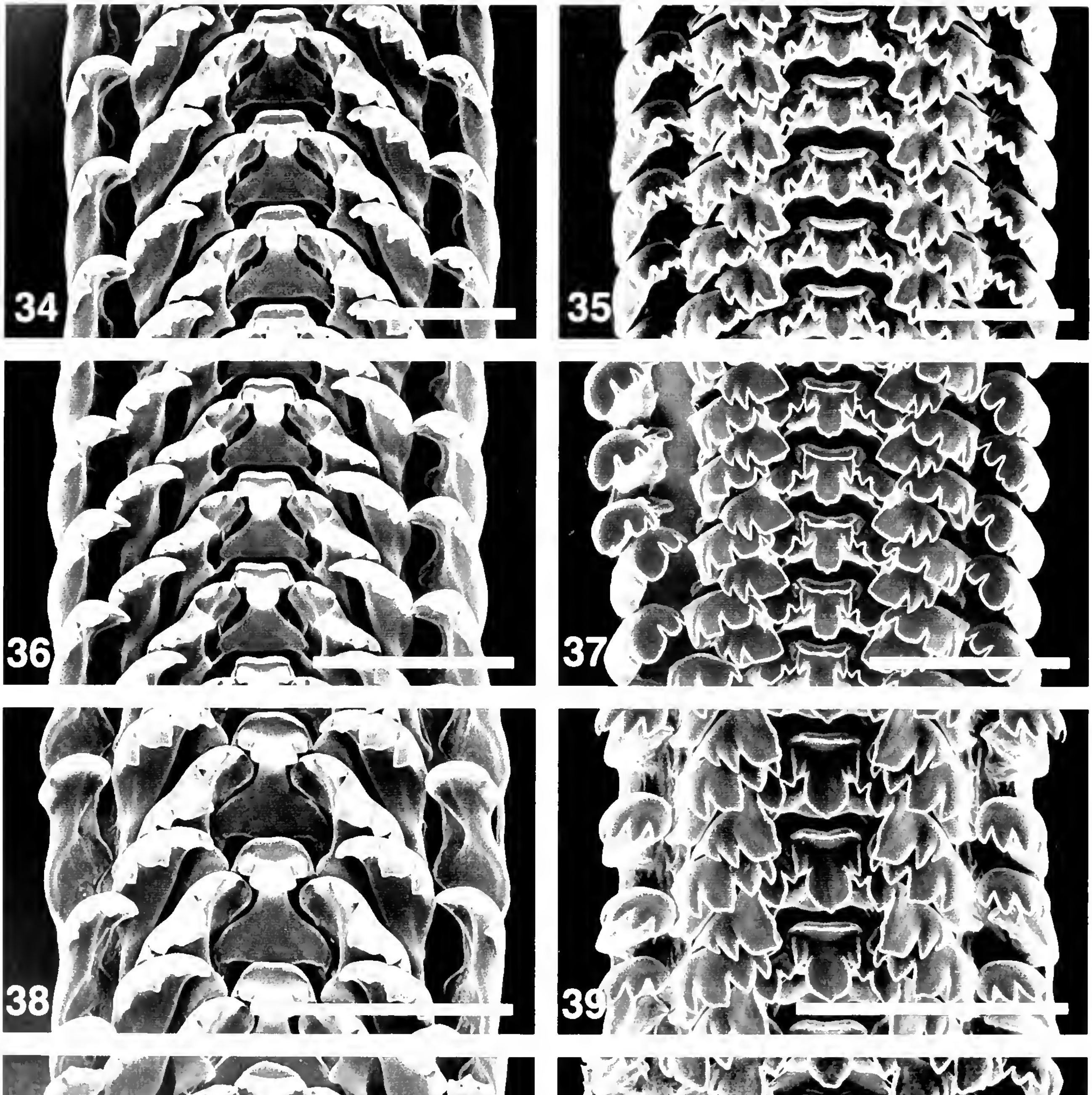
Figures 23–33. Penes and paraspermatozoa of *Littoraria filosa* and *Littoraria delicatula*. **23–30.** Penes of *L. filosa*. **23–26.** Julago Beach, Cape Leveque, Western Australia (BMNH 20010120; shell H = 20.8 mm, 20.8 mm, 19.8 mm, 18.7 mm). **27, 29.** Lookout Hill, Broome, Western Australia (BMNH 20010121; shell H = 19.7 mm, 15.8 mm). **28.** Mangrove Point, Roebuck Bay, Broome, Western Australia (BMNH 20010122; shell H = 21.1 mm). **30.** Withnell Bay, Burrup Peninsula, Western Australia (BMNH 20010141; shell H = 18.3 mm). **31–33.** Penes and paraspermatozoa of *L. delicatula*, Bodra Kaal, Chavlabogi, Sundarbans, Bangladesh (BMNH 20010123; shell H = 14.1 mm, 11.3 mm). Dotted line indicates extent of opaque glandular portion of penial glandular disc.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torinopsis occur and for which visual selection by predators has been suggested as a possible explanation for the maintenance of the polymorphism, which is assumed to have a genetic basis (Cook, 1986a, b, 1992; Reid, 1987). The same process could possibly maintain these rare, local cases of polymorphism in the normally monomorphic *L. carinifera*; a similar explanation has been proposed for local polymorphism in *L. intermedia* by Cook and Bridle (1995). However, it should be noted that like almost all others in the genus, this species has planktotrophic development and therefore the potential for wide gene flow; selection on local populations would therefore have to be strong, or gene flow would have to be restricted in some way, in order to achieve local genetic differentiation of polymorphic populations. A similar case of local polymorphism has been found in *L. melanostoma* (see above).

Littoraria (*Palustorina*) *sinensis* (Philippi, 1847)
(Figures 38–52, 56–64, 68)

Litorina sinensis Philippi, 1847: 16–17, *Litorina* pl. 6, fig. 23 (China; lectotype (Reid, 1986a) MNHN + 2 paralectotypes, seen, Figures 42, 43). Lischke, 1871b: 71–72. Weinkauff, 1882: 83–84, pl. 11, figs 9, 12.
Littorina intermedia var. *sinensis*—Nevill, 1885: 147.
Littorina sinensis—Pilsbury, 1895: 62.
Litorina strigata Lischke, 1871a: 148–149 (Nagasaki, Japan; types lost; not *Littorina intermedia* var. *strigata* Philippi, 1846 = *Littoraria strigata*). Lischke, 1871b: 73, pl. 5, fig. 22 (not Philippi, 1846).
Littorina strigata (Lischke)—Pilsbry, 1895: 62 (not Philippi, 1846).
Littorina (*Melaraphe*) *strigata* (Lischke)—Tryon, 1887: 245, pl. 43, fig. 33 (not Philippi, 1846).
Littorinopsis strigata (Lischke)—Kuroda and Habe, 1952: 64 (not Philippi, 1846). Oyama and Takemura, 1961, fig. 10 (not Philippi, 1846).
Littoraria strigata (Lischke)—Kojima, 1958 (egg capsule; not Philippi, 1846). Azuma, 1960: 10 (not Philippi, 1846). Higo, 1973: 46 (not Philippi, 1846).
Littoraria strigata ('Dunker')—Yoo, 1976: 56, pl. 7, figs 18, 19 (not Philippi, 1846).
Littoraria scabra strigata (Lischke)—Higo and Goto, 1993: 74 (not Philippi, 1846).
? *Littorina adonis* Yokoyama, 1927: 451, pl. 51, fig. 8 (Koyasu, southern Musashi, Japan; Upper Musashino [Pliocene: Rosewater, 1970]; holotype, Geological Institute, University of Tokyo; not seen). Rosewater, 1970: 453, pl. 349, figs 8, 9.
Littoraria adonis—Okutani, 1986: 71, fig. unnumbered.
Littorina (*Littorinopsis*) *scabra scabra*—Rosewater, 1970: 456–461 (in part; not Linnaeus, 1758 = *Littoraria scabra*).
Littorina scabra.—Cai, 1991: 51, fig. 43 (not Linnaeus, 1758).
Littoraria (*Palustorina*) *articulata*.—Reid, 1986a: 200–209, figs 90c–e, 92h–i (penes), 93e (egg capsule), 94 (in part; not *Littorina intermedia* var. *articulata* Philippi, 1846 = *Littoraria articulata*). Choe, 1992: 289–290, fig. 54 (not Philippi, 1846). Reid, 1992a: 195–197, fig. 4g (in part; not Philippi, 1846). Higo et al., 1999: 92.
Palustorina (sic) *articulata*.—Fukuda et al., 1992: 57, pl. 9, figs 129a, b (not Philippi, 1846).

Nomenclature: The nomenclature of this species has suffered numerous changes. The name *Littorina sinensis* has seldom been used (most recently by Pilsbry, 1895). It was redescribed as *Litorina strigata* by Lischke (1871a) and this name became familiar in various combinations in the Japanese literature of the mid-twentieth century. Rosewater (1970) combined it with some 20 other species under the name *Littorina scabra*. The Pliocene fossil *Littorina adonis* has not been examined, but is probably this species, and the name was used for Recent Japanese specimens by Okutani (1986). It has become generally known as *Littoraria articulata* following Reid (1986a), but that taxon is here shown to consist of two species. As discussed below, the only entirely diagnostic character is the penis, although the majority of shells can be confidently identified. Although the lectotype is a dry shell, the form of the aperture and columella, and the diffuse color pattern on the shoulder region, are typical of the present species.

Material Examined: Types as indicated; 14 lots; 35 penes; 1 sperm sample; 12 pallial oviducts; 5 radulae.

Shell (Figures 42–52): Adult size range 6.3–20.6 mm. Shape high-turbinate to elongate (H/B = 1.28–1.73; SH = 1.57–2.05); whorls rounded, suture impressed, periphery of last whorl slightly or not at all angled; moderate thickness. Mature lip not flared; columella pillar concave, excavated; inner lip of aperture sharply raised adjacent to base of columella. Sculpture of (7)8–9 primary spiral grooves on spire whorls; intervening ribs usually remain undivided, numbering 20–23 on last whorl; occasionally some ribs may be divided by an impressed line and become more numerous; ribs of equal width above periphery, slightly narrower on base; grooves are impressed lines on spire whorls, becoming deeper and wider on last whorl, commonly up to half width of intervening ribs at periphery of whorl (rarely equal to rib width); in smoothest shells grooves remain as impressed lines only. Microsculpture of faint spiral striae over rib surface, with axial microstriae in grooves. Protoconch 0.35 mm diameter, 3.5 whorls, with spiral

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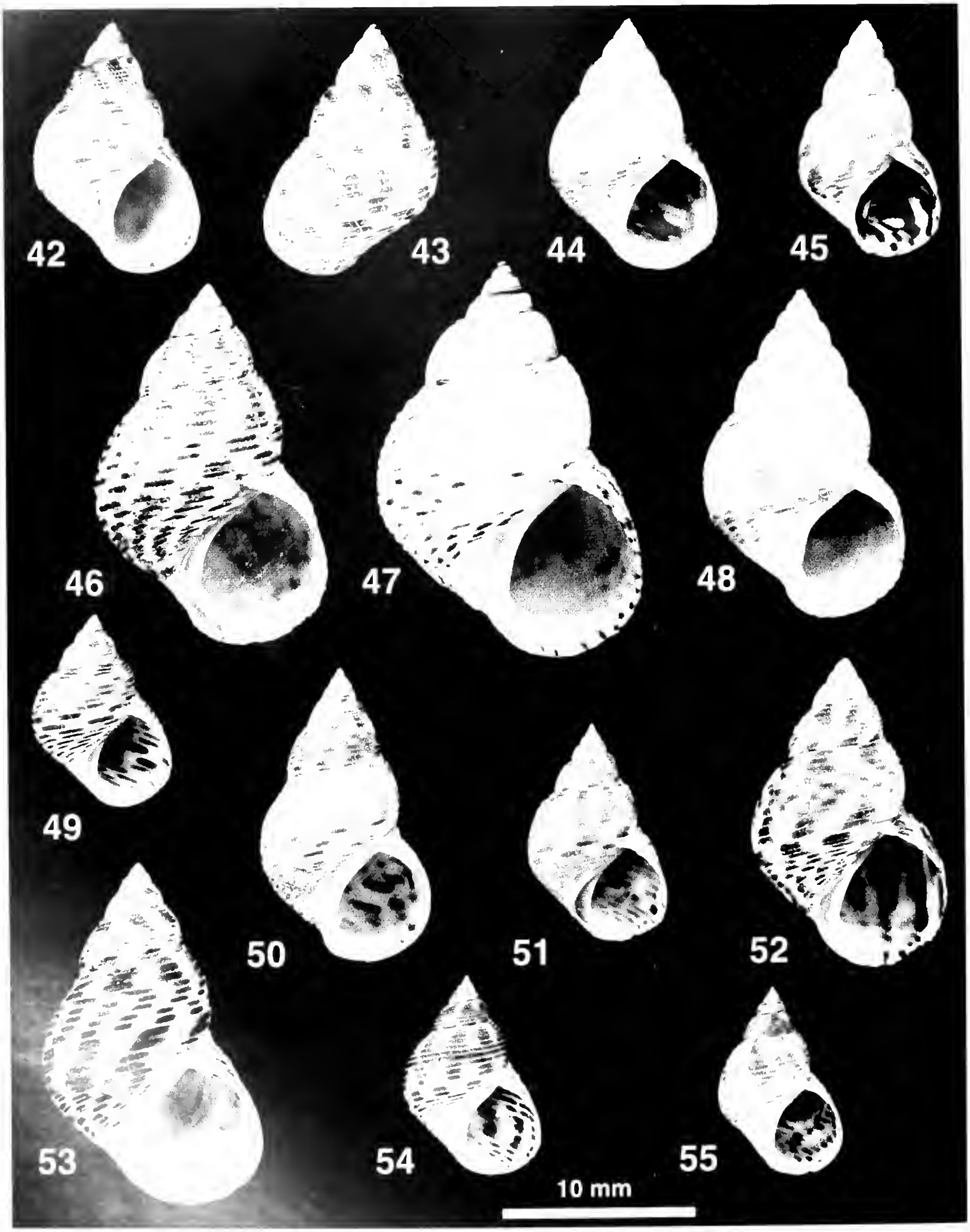
Figures 34–41. Radulae of *Littoraria* species. **34, 35.** *L. bengalensis* new species, paratype, Hare Island, Gulf of Mannar, Tamilnadu, India (BMNH 20000755, shell H = 16.3 mm; flat view and 45° from anterior). **36, 37.** *L. delicatula*: Bodra Kaal, Chaylabogi, Sundarbans, Bangladesh (BMNH 20010123, shell H = 14.4 mm; flat view and 45° from anterior). **38–41.** *L. sinensis*. **38, 39.** Mangrove trees, Tan Shui, Taipei, Taiwan (BMNH 20010130, shell H = 11.1 mm; flat view and 45° from anterior). **40, 41.** Rocks, Kafuri, Maebaru City, Kyushu, Japan (BMNH 20010131, shell H = 15.5 mm; flat view and 45° from anterior). Scale bars = 100 µm.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ribs and sinusigera notch. Color variable: cream with pattern of orange brown to dark brown dashes on ribs, with whitish dashes between; degree of axial alignment of dashes varies from diffusely tessellated or marbled pattern with alignment into short axial stripes at suture and periphery only (Figures 43, 44, 51) to the rare more complete alignment in oblique axial stripes (Figure 46); pattern often emphasizes 2–3 ribs at periphery. Columella purple brown or white; aperture cream with exterior pattern showing through.

Animal: Headfoot, operculum, paraspermatozoa, pallial oviduct and radula do not differ significantly from those of *L. articulata* as described by Reid (1986a). As in *L. articulata* (Reid and Mak, 1999: fig. 4C, D) the radula shows likely phenotypic plasticity and differs in tooth shape on rock and wood substrates (compare Figures 39 and 41). Penis (Figures 56–64) not bifurcate, small glandular disc incorporated into distal end of wrinkled base; smooth narrowly elongate filament 0.3–0.5 total length of penis; penial vas deferens an open groove to filament tip. Pelagic egg capsule a lens-shaped biconvex disc without peripheral flange, 350 μm diameter, containing single ovum about 70 μm diameter (Kojima, 1958: fig. 2a, b; reproduced in Reid, 1986a: fig. 93c). Development planktotrophic.

Distribution: Habitat in littoral fringe on rock (including granite boulders and concrete sea walls) in both sheltered and moderately exposed situations; also on trunks at seaward edge of mangrove forests (published accounts of the ecological distribution of '*Littorina scabra*' on the rocky shores of Hong Kong and southern China probably refer to a mixture of this species and *L. articulata*, e.g. Chambers, 1980; Ohgaki, 1985; Yi and Li, 1988; You, 1990). Range (Figure 68): from southern China to Yellow Sea, South Korea, Kyushu and Seto Inland Sea, perhaps Ryukyu Islands. Records: China: Macao (BMNH); Hong Kong (Shek O; Deep Bay; Tai Po; Three Fathoms Cove; Hoi Ha, Mirs Bay; Wu Kwai Sha; Aberdeen; all BMNH); Xiamen (Hai Cang; Gulayang, both BMNH); Spider Island, Fujian (USNM); Zhenhai, Ningbo River (BMNH); Shawaishan, mouth of Yangtze River (BMNH); Qingdao (Tai Ping; Huan Dao; Hui Quan; all BMNH). Taiwan: Tan Shui (BMNH). Japan: Ryukyu Islands (USNM); Kagoshima (BMNH); Amakusa (USNM, NSMT); Matsuura, Nagasaki Pref. (BMNH); Hirado (AMS); Maebaru City (BMNH); Ehime Pref. (USNM); Kasaoka, Okayama Pref. (USNM); Nagae River, Okayama City (BMNH); Yoshino River, Tokushima City (BMNH). South Korea: Sachun Kun, Kyongsang Namdo (ANSP).

Remarks: Reid (1986a) concluded that *L. articulata* was a single species extending from Australia to India and Japan, but with two geographical forms of more restricted distribution, one from northwestern Australia and the other from China and Japan. The latter was characterised by stronger sculpture, a more diffuse pattern and it was said that the penial filament was sometimes relatively longer than in specimens from South East Asia and Australia. It was also noted that the egg capsule of the Japanese form described by Kojima (1958) was larger than that of *L. articulata* from Queensland and lacked the circumferential flange. However, with little information on the range of intraspecific variation the significance of the difference in capsule shape was unclear. The eastern Asian form was 'tentatively assigned to *L. articulata*', but it was suggested that further work was required.

Since then, much additional material has been gathered. It has been found that all specimens from northern China, Korea and Japan share the longer penial filament. Most significant, however, is the discovery that the 'typical form of *L. articulata* and the eastern Asian form' occur syntopically at several localities in southern China around Hong Kong and Xiamen. At these localities the penial differences remain distinct (e.g. Figures 57, 58 and 65, 66, from a locality in Hong Kong) and are correlated with small, but consistent, differences in shell shape, sculpture and color. This leaves no doubt that the 'forms' are separate species.

The differences between *L. articulata sensu stricto* and *L. sinensis* are summarised in Table 2. The most useful and entirely diagnostic character is the shape of the penis: in *L. sinensis* (Figures 56–64) the penial filament is 0.3 to 0.5 of the entire penial length (less than 0.2 in *L. articulata*, Figures 65–67) and the glandular disc is usually about half the size and less swollen. No other anatomical differences have been discovered, so that morphological identification of juveniles and females must rely on features of the shell.

It is possible that the differences in egg capsule shape mentioned above may prove to be consistent. Capsules in this group have been illustrated three times. Reid (1986a) showed capsules of *L. articulata* s.s. from north Queensland with a circumferential flange (diameter 248–268 μm, ovum about 65 μm). Those illustrated by Mak (1995) from Hong Kong were of similar shape, but

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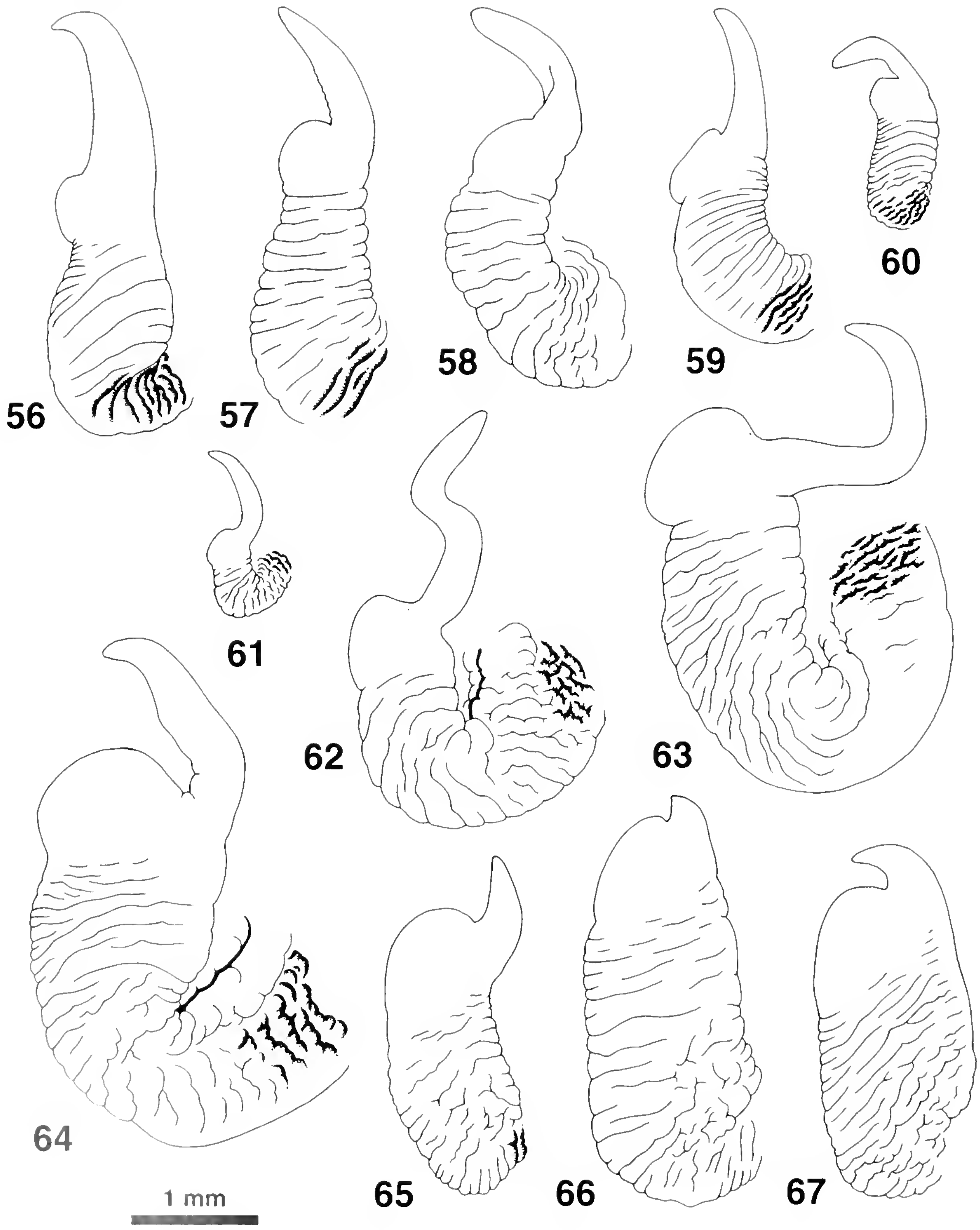
Figures 42–55. Shells of *Littoraria sinensis* and *Littoraria articulata*. **42–52.** *L. sinensis*. **42, 43.** Lectotype of *Littorina sinensis* (Philippi, 1847), China (MNHN). **44.** Hoi Ha, Mirs Bay, Hong Kong (BMNH 20010124). **45.** Tai Ping Bay, Qingdao, China (BMNH 20010125). **46.** Tai Po, Hong Kong (BMNH 20010126). **47.** Yoshino River estuary, Kanazawa, Tokushima City, Shikoku, Japan (BMNH 20010127). **48.** Shuanzm, Shangai, China (BMNH 20010128). **49.** Hai Cang, Xiamen, China (BMNH 20010129). **50.** Tan Shui, Taipei, Taiwan (BMNH 20010130). **51.** Aberdeen, Hong Kong (BMNH 20010132). **52.** Katiri, Maebaru City, Kyushu, Japan (BMNH 20010131). **53–55.** *L. articulata*. **53.** Tai Po, Hong Kong (BMNH 20010138). **54, 55.** Aberdeen, Hong Kong (BMNH 20010137).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1 mm

Table 2. Summary of differences between *Littoraria sinensis* and *L. articulata* (shell characters apply to specimens from north-western Pacific Ocean only).

Character	*Littoraria sinensis*	*Littoraria articulata*
Shell shape	Relative spire height can be taller (to 2.05); whorls slightly more rounded	Does not attain such tall spire (relative spire height to 1.89); whorls flatter
Shell sculpture	Grooves up to half to one times rib width; small shells can be almost smooth	Grooves up to one quarter rib width; small shells can be almost smooth
Columella	Shorter and more concave, giving more oval aperture; narrower; inner lip of aperture more sharply raised	Longer, straighter, giving ear-shaped aperture; inner lip of aperture less sharply raised
Shell color	Paler, often indistinctly clouded pattern; alignment of dashes less marked	Darker; distinct dashes, well aligned into axial stripes at suture and periphery
Penis	Penial filament 0.3–0.5 total length of penis	Penial filament less than 0.2 total length of penis
Distribution	China, Korea, Japan	Southern China to India and Australia

larger (diameter 300–340 µm, ovum 69–71 µm). The capsule of *L. sinensis* from Amakusa, Kyushu, shown by Kojima (1958) was a simple lens shape without a peripheral flange (diameter 350 µm, ovum about 70 µm). Mak (1995) showed that in three *Nodilittorina* species egg capsule diameter varied by 39 to 53% and suggested that shape and sculpture are more consistently diagnostic of species than size. It is possible that the capsules he illustrated as '*L. articulata*' were indeed of that species rather than the sympatric *L. sinensis*, despite their large size, so that shape might be relatively constant within this species across its geographical range, but this remains to be investigated. Caution is necessary, however, since capsules swell and the flange becomes less noticeable between spawning and hatching (Berry, 1986, in *L. strigata*; Ho, 1987). The capsules shown by Reid (1986a) and Kojima (1958) are very similar respectively to the early and late (24 hours after spawning) capsules of *L. strigata* (Berry, 1986: fig. 1) and might not represent genuine interspecific differences.

The characteristic features of the shells of *L. sinensis* and *L. articulata* are difficult to describe or quantify, owing to considerable intraspecific variation. Nevertheless, with experience sympatric samples can usually be successfully identified (as confirmed by penial shape of males) from their shells. The size range is similar (maximum 20.6 mm in *L. sinensis*, 19.0 mm in *L. articulata*) and both attain larger size in mangrove habitats than on rocky shores. Overall shape is also similar, but examples of *L. sinensis* can attain a slightly taller spire (relative spire height up to 2.05, cf. 1.89 in *L. articulata*) and the whorls are a little more rounded. In *L. articulata* the columellar pillar is longer and straighter, so that the aperture appears more ear-shaped. In contrast the columella of *L. sinensis* is slightly shorter and a little concave, and the aperture therefore more nearly oval. The columella of *L. sinensis* is usually narrower, but still deeply excavated, and the inner lip of the aperture (adjacent to the concavity of the columella) is more sharply raised, sometimes so much so that a slight umbilical crack is present. Both species share a similar count of primary grooves and of ribs on the body whorl, and both sometimes display dwarf forms with smooth shells in which grooves are present only as impressed lines. However, in larger and more strongly sculptured examples the grooves of *L. sinensis* are always more pronounced (up to half of, or even equal to, width of intervening ribs, compared with maximum of one quarter of rib width in *L. articulata*) and such shells are unmistakable (Figures 46, 47).

Shell color and pattern are likewise difficult to characterise, but often assist identification. *Littoraria sinensis* is usually paler, typically with a more finely mottled or tessellated or indistinct 'clouded' pattern, in which whitish flecks are present between the darker dashes. In both species the dashes are more or less aligned into oblique axial series, although this is usually only pronounced at the suture and periphery of each whorl, giving rise to short axial stripes at these points. This alignment is often more developed in *L. articulata*, in which, at the periphery, the axial stripes extend across four of the spiral ribs (Figures 53, 54); in *L. sinensis* this alignment more often covers only two or three peripheral ribs (Figures 50, 51).

These contrasting shell characters are emphasized by the figures of sympatric samples of the two species (Fig-

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Figures 56–67. Penes of *Littoraria sinensis* and *Littoraria articulata*. **56–64.** *L. sinensis*. **56.** Tan Shui, Taipei, Taiwan (BMNH 20010130, shell H = 11.0 mm). **57, 58.** Shek O, Hong Kong (BMNH 20010133; shell H = 8.6 mm, 9.4 mm). **59.** Hai Cang, Xiamen, China (BMNH 20010129, shell H = 9.0 mm). **60.** Huan Dan, Qingdao, China (BMNH 20010134). **61.** Okayama Port, Kojima Bay, Japan (BMNH 20010135, shell H = 7.2 mm). **62–64.** Nagae River estuary, Otogo, Okayama City, Japan (BMNH 20010136; shell H = 13.8 mm, 13.0 mm, 14.0 mm). **65–67.** *L. articulata*. **65, 66.** Shek O, Hong Kong (BMNH 20010139; shell H = 8.7 mm, 10.2 mm). **67.** Aberdeen, Hong Kong (BMNH 20010137). Dotted line indicates extent of opaque glandular portion of penial glandular disc.

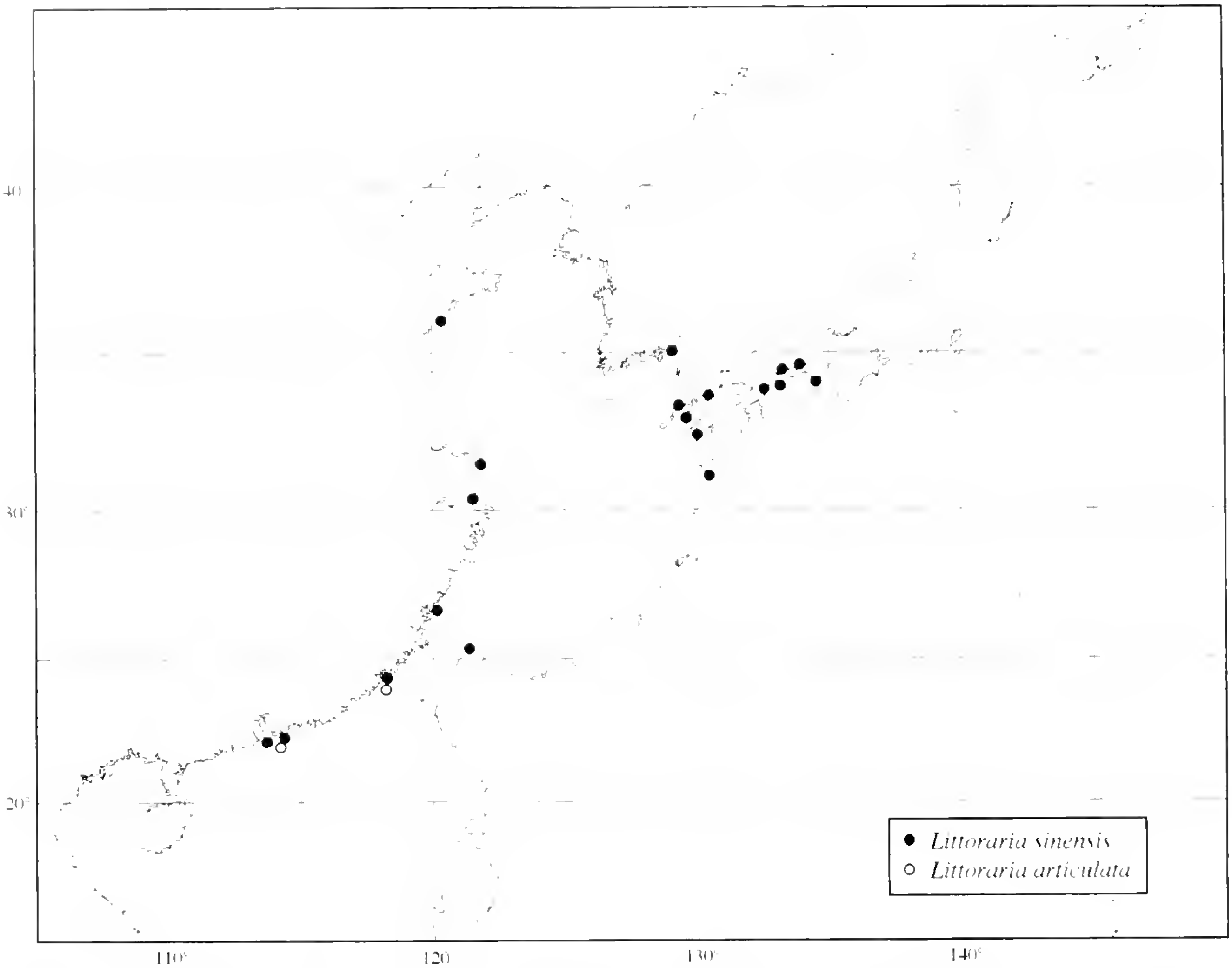

Figure 68. Geographical distribution of *Littoraria sinensis* with, for comparison, the records of *Littoraria articulata* from the same area (see text for lists of records).

ures 46 and 53; Figures 51, 54, 55). Nevertheless, shells of the two can sometimes appear virtually identical (e.g. Figures 44, 55) and only penial shape is reliably diagnostic. Geographical locality can also aid identification, since the distributions are known to overlap only between Hong Kong and Xiamen (Figure 68). In Hong Kong the sites of recorded syntopy are Shek O, Tai Po, Three Fathoms Cove, Wu Kwai Sha and Aberdeen, and Hai Cang near Xiamen (all BMNH). These sites range from mangroves to moderately exposed granite boulders and both species are common, so that there is no evidence for different habitat preferences.

Littoraria sinensis is also closely similar to *L. strigata*, distributed from the Philippines and southern Vietnam to Indonesia, Malaysia and India. The features of shell shape and coloration described above also distinguish *L. sinensis* from *L. strigata*: the latter often has a more strongly aligned pattern of oblique axial stripes, and sculpture is weaker than in *L. sinensis*. Most importantly, the penial filament of *L. strigata* is long, tapering and vermiform, 0.6 to 0.7 of the total penial length (Reid, 1986a).

Littoraria (Palustorina) articulata (Philippi, 1846)
(Figures 53–55, 65–68)

Synonymy as in Reid (1986a), excluding the entries now listed under *L. sinensis* above.

Distribution: Records listed in Reid (1986a) from China and Japan all either apply to *L. sinensis* or the identification is doubtful. The following new records (all BMNH) have all been verified by anatomical examination: China: Hai Cang, Xiamen; Hong Kong (Tai Po; Aberdeen; Shek O; Three Fathoms Cove; Beigang Island); Hainan. Vietnam: Sung Sot Cave, Ha Long Bay; Do Son, near Haiphong. Cambodia: Koh Pouree, off Sihanoukville. The species is abundant at localities all around Singapore (St Johns Island, Changi Point, Sentosa; East Coast Park; Sarimbun; all BMNH), whereas the similar

species *L. strigata* is rare (see below). Only a single preserved animal of the *L. articulata/strigata* group has been seen from the Indian subcontinent; this specimen, from Bombay, was a male of *L. strigata* (see below), so the occurrence of *L. articulata* in the region remains to be verified. A single shell has been seen from Bandar-e-Khamir, west of Bundar Abbas, Iran (BMNH), with a color pattern resembling *L. articulata*. This would represent a range extension of either *L. articulata* or *L. strigata*, but positive identification requires anatomical examination.

Littoraria (Palustorina) strigata (Philippi, 1846)

Littoraria strigata—Berry, 1986:144–149, fig. 1 (egg capsule).

Distribution: Additional material from South East Asia supports the suggestion that this species predominates in localities with clearer water, whereas the similar *L. articulata* is present in more turbid and estuarine sites in the region. The occurrence of this species in the Arabian Sea has been confirmed by a single male specimen from Bombay. The species is uncommon in Singapore, where *L. articulata* is abundant. New records (all BMNH): Singapore: Sarimbun; St John's Island; Changi Point. Malaysia: Kudat, Sabah. Thailand: Krabi. India: Colaba, Bombay.

Remarks: Nine additional ethanol-preserved samples have been seen, supporting the earlier conclusion that this is indeed a species distinct from *L. articulata*. The only diagnostic morphological character remains the shape of the penis, in which the filament is 0.6 to 0.7 of the total length.

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This work was stimulated by the conjunction of a number of events: the unexpected discovery of an undescribed *Littoraria* species in northern Australia by M. Stuckey in 1998 (Stuckey and Reid, in prep.), questions from H. Fukuda about the identification of the Japanese '*L. articulata*' and my own observation of assortative mating and differential zonation between 'forms' of '*L. intermedia*' in south India. In addition, there was a growing realisation that very small but consistent differences in penial form could be of taxonomic significance (Reid, in press, a). Since 1985 I have examined much additional material of *Littoraria*, both personally collected and kindly sent to the BMNH by colleagues. My grateful thanks to those who have provided specimens for this study: G. Feulner (Dubai), H. Fukuda (Okayama University), E. Glover (BMNH), D. Kadolsky (London), Y. M. Mak (Hong Kong), A. Matsukuma (Kyushu University), G. Pendred (Portsmouth), M. Stuckey (University of Western Australia), J. D. Taylor (BMNH). V. Héros (MNHN) kindly sent a type on loan. I thank the Tropical Marine Mollusc Programme of Danida (Denmark) for the opportunity to carry out fieldwork in India.

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Phylogeny of pneumostomal area morphology in terrestrial Pulmonata (Gastropoda)

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ABSTRACT

Mapping pneumostomal area morphological character states on the phylogenetic tree generated by a recent ribosomal RNA sequence study allows an independent estimate of the course of pneumostomal area evolution and shows to what extent the RNA sequence data supports evolutionary events previously hypothesized for pneumostomal area characters. A breathing channel without a valve, an open rectal termination, a closed secondary ureter, and a simple pneumostomal excretory route are plesiomorphic within Stylommatophora. Multiple homoplasy is evident.

Additional key words: Mollusca, land snail, anatomy, phylogenetic systematics, parsimony.

INTRODUCTION

The molecular phylogenetic analysis of Wade et al. (2001) examined nucleotide sequences of the ribosomal RNA gene cluster of over 100 species of Stylommatophora, representing 50 families plus out-groups. That study supported the monophyly of Stylommatophora found by previous analyses (e.g., Emberton et al., 1990; Wade and Mordan, 2000). Its other significant findings include (1) a fundamental dichotomy between an "achatinoid clade" (including Achatinidae, Subulinidae, and Streptaxidae) and all remaining ("non-achatinoid") stylommatophorans; (2) the monophyly of many traditional family groups is supported; and (3) the orthurethran condition, long presumed to be plesiomorphic in Stylommatophora, is most likely a derived state. Wade et al. (2001) only briefly considered morphological characters other than those typifying the traditional groups Orthurethra, Mesurethra, and Sigmurethra. Morphological correlates, if they exist, have yet to be discovered for many of the deep branches of their phylogenetic tree (Wade et al., 2001: fig. 1). For example, there appears to be no extant, single morphological character state that is autapomorphic for either the "achatinoid clade" or the "non-achatinoid clade" (P. Mordan, personal communication, 2001). It is intrinsically interesting, for understanding the history and mode of pulmonate evolution and to increase the liaison between molecular and morphological data sets, to plot the distribution of morphological character states on the phylogenetic tree generated by molecular analysis.

Goodfriend (1986), examining the lower course of the secondary ureter in *Sagda* Beck, 1837, observed that the ureteric region of the pneumostome might prove to be taxonomically useful. Emberton (1991) included several pneumostomal area characters in his phylogenetic analysis of 17 subfamilies of Stylommatophora. Suvorov (2000) studied the pneumostomal area of terrestrial pulmonate gastropods and provided an analysis of four principal characters, each having from two to seven mutually exclusive states. He described the distribution of these character states across 34 families and hypothesized transformation series, based on a process of functional analysis. There is moderately good overlap between the array of taxa examined by Suvorov (2000) and that analyzed by Wade et al. (2001).

In this paper, the pneumostomal character states described by Suvorov (2000) are mapped on the phylogenetic framework generated by the Wade et al. (2001) study. This allows an independent estimate of the course of pneumostomal area evolution and shows to what extent the RNA sequence data supports the evolutionary inferences of Suvorov. Essentially the same method was employed by Roth (1996) to estimate the history underlying the absence of dart sac and other reproductive organs in several genera of Helminthoglyptidae.

MATERIALS AND METHODS

Taxa: Table 1 lists the stylommatophoran species studied by Suvorov (2000) and their family assignments. Suvorov's results and discussion are presented in terms of families rather than species; the implication—although it is not explicitly stated—is that he found pneumostomal area characters to be constant within a family.

Nearly all of these families were included in the mo-

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Table 1. Stylommatophoran species studied by Suvorov (2000), and taxon codes used in this study. Taxonomy and order of taxa as in original, except as noted. Families without indicated codes are not cladistically analyzed herein.

Succineidae (**SUC**)
Succinea putris (Linnaeus, 1758)
Oxyloma sarsi (Esmark, 1886)
Succinella oblonga (Draparnaud, 1801)
Partulidae (**PAR**)
Partula otaheitana (Bruguière, 1792)
Clausiliidae (**CLA**)
Macrogastra ventricosa (Draparnaud, 1801)
Mentissa gracilicosta (Rossmässler, 1836)
Scrobifera taurica (Krynicki, 1837)
Serrulina serrulata (L. Pfeiffer, 1847)
Subulinidae (**SUB**)
Subulina octona (Bruguière, 1789)
Rumina decollata (Linnaeus, 1758)
Glessula ceylonica (L. Pfeiffer, 1845)
Ferussaciidae
Amphorella melampoides (Lowe, 1834)
Achatinidae (**ACH**)
Achatina fulica (Bowdich, 1822)
Orthalicidae (**ORT**)
Liguus fasciatus (Müller, 1774)
Acavidae (**ACA**)
Acavus phoenix (L. Pfeiffer, 1854)
Sagdidae (**SAG**)
Sagda cookiana (Gmelin, 1791)
Ceriidae (**CER**)
Cerion uva (Bruguière, 1792)
Cochlicopidae (**COC**)
Cochlicopa lubrica (Müller, 1774)
Cochlicopa nitens (Gallenstein, 1852)
Orculidae (**ORC-1, ORC-2**)*
Sphyradium doliolum (Bruguière, 1792)
Euxinolauria zonifera (Pilsbry, 1934)
Lauria cylindracea (Da Costa, 1778)
Chondrinidae (**CHO**)
Chondrina rhodia taurica (Kessler, 1860)
Chondrina clienta caucasica Ehrmann, 1931
Pyramidulidae (**PYR**)
Pyramidula rupestris (Draparnaud, 1801)
Enidae** (**ENI**)
Rachis tulearensis Fischer-Piette, 1964
Merdigera obscura (Müller, 1774)
Ena montana (Draparnaud, 1801)
Brephulopsis cylindrica (Menke, 1828)
Caucasicola raddei Kobelt, 1880
Bradybaenidae (**BRA**)
Bradybaena fruticum (Müller, 1774)
Hygromiidae (**HYG**)
Xeropicta derbentina (Krynicki, 1836)
Xeropicta krynickii (Krynicki, 1833)
Monachoides vicina (Rossmässler, 1842)
Helicodontidae
Oestophora barbula (Rossmässler, 1838)
Helicidae (**HEL**)
Cepaea vindobonensis (Férussac, 1821)
Helix albescens Rossmässler, 1839
Helminthoglyptidae
Helminthoglypta arrosa (W. G. Binney, 1858)
Humboldtianidae
Humboldtiana sp.

Table 1. Continued

Sphincterochilidae
Sphincterochila candidissima (Draparnaud, 1801)
Epiphragmophoridae
Epiphragmophora diluta (L. Pfeiffer, 1842)
Endodontidae (**END**)
Ruthvenia clathratula (L. Pfeiffer, 1850)
Discidae (**DIS**)
Discus ruderatus (Studer, 1820)
Polygyridae (**POL**)
Polygyra septemvolva Say, 1818
Zonitidae (**DAU**, in part)
Oxychilus mingrelicus (Mousson, 1863)
Oxychilus duboisi (Mousson, 1863)
Aegopis verticillus (Lamarck, 1822)
Daudebardiidae (**DAU**, in part)
Inguria wagneri (Rosen, 1911)
Parmacellidae
Parmacella ibera Eichwald, 1841
Gastrodontidae
Zonitoides nitidus (Müller, 1774)
Ariophantidae (**ARP**)
Bensonies nepalensis (Blanford, 1904)
Haplotrematidae (**HAP**)
Haplotrema minimum (Ancey, 1888)
Limacidae (**LIM**)
Limax maculatus (Kaleniczenko, 1851)
Bielzia coerulans (Bielz, 1851)
Arionidae (**ARI**)
Arion lusitanicus Mabille, 1868
Arion fasciatus (Nilsson, 1823)

* Orculidae *sensu* Suvorov (2000) is polyphyletic. ORC-2 represents a clade comprising *Lauria* species (assigned to Pupillidae by Wade et al., 2001).
** Enidae is called Buliminidae by Wade et al. (2001).
*** Suvorov (2000: 91) without justification introduced the combination *Ancotrema minimum* for this taxon.

lecular analysis of Wade et al. (2001; Table 1), although in many cases with different species as exemplars. Based on the finding that most traditional family groups hold together as monophyletic units in molecular analysis (Wade et al., 2001: 118), I here proceed on the assumption that—with a few exceptions noted below—the families of the Suvorov and Wade et al. analyses can be treated as equivalent, and that character states observed to be true for a family by Suvorov can be regarded as true for the same nominal family represented on the phylogenetic tree of Wade et al. This assumption can, of course, be tested by dissection of the Wade et al. exemplar species that were not examined by Suvorov.

Figure 1 replicates the branching structure of Wade et al.'s (2001: fig. 1) neighbor-joining phylogenetic tree, with respect to the taxa studied by Suvorov. The tree is further simplified by being drawn as a cladogram rather than a phylogram; in other words, branch lengths, which in the original reflect genetic distances among taxa, have no significance in this figure. On the original tree, some details of the first- and second-order branching directly

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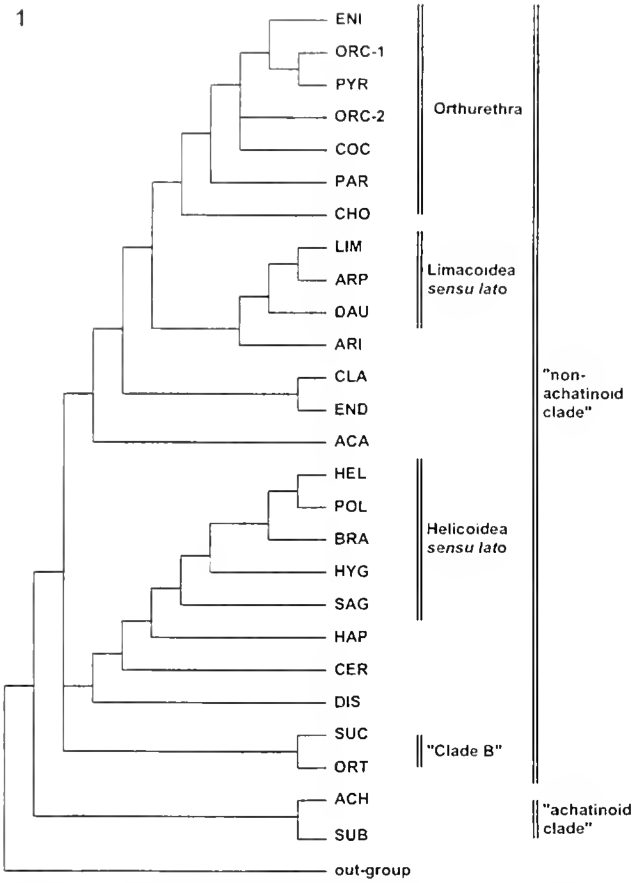

Figure 1. Cladogram based on the molecular phylogenetic hypothesis of Wade et al. (2001), simplified to include only taxa studied by Suvorov (2000), and showing the extent of higher clades referred to in text: "achatinoid clade" and "non-achatinoid clade" of Wade et al. (2001), Orthurethra Pilsbry, 1900; Limacoidea *sensu lato* of Hausdorf (1998); Helicoidea *sensu lato* and "Clade B" of Roth and Sadeghian (in press). Taxon codes as in Table 1.

above the "achatinoid"-"non-achatinoid" dichotomy are supported by relatively few characters and may not be corroborated by future studies.

The following taxa could not be placed on the cladogram: Epiphragmophoridae, Ferussaciidae, Gastrodontidae, Helicodontidae, Helminthoglyptidae, Humboldtianidae, Parmacellidae, and Sphincterochilidae. Wade et al. (2001) included "Helminthoglyptidae," but their exemplar *Monadenia fidelis* (Gray, 1834), is a species of Bradybaenidae. Both Suvorov (2000) and Wade et al. (2001) treated *Oxychilus* Fitzinger, 1833, as a genus of Zonitidae. In his phylogenetic analysis of Limacoidea *sensu lato*, Hausdorf (1998) placed *Oxychilus* in Daudebardiidae and the clade exemplified by it is so labeled herein.

Wade et al. (2001) included no Sagdidae. Emberton's (1991) cladistic analysis revealed a clade comprising *Thysanophora* Strebel and Pfeffer, 1880 (Thysanophoridae); the New World "camaenid" *Pleurodonte* Fischer von Waldheim, 1807; and the sagdid genera *Sagda* and *Aquaebana* Pilsbry, 1926. These taxa are united by the synapomorphies of right parietal and visceral ganglia fused and right parietal and right pleural ganglia fused. *Pleurodonte* and the sagdid genera are further united by the synapomorphy of left parietal and left pleural ganglia fused (Emberton, 1991: 218). Based on these findings, Sagdidae is tentatively placed on the cladogram in the position of New World "Camaenidae," exemplified in the Wade et al. analysis by *Polydontes* Montfort, 1810.[2] However, Goodfriend (1986) observed that the distinctive features of the sagdid pneumostomal area are not shared by Pleurodontidae such as *Labyrinthus* Beck, 1837, and *Pleurodonte*.

Wade et al. (2001) included no Endodontidae; their analysis resolved an "endodontoid clade" consisting of members of Punctidae, Charopidae, and Otoconchidae, but another traditionally "endodontoid" family, Discidae, fell into a distinct clade of its own. Endodontidae is tentatively placed on the cladogram in the position of the "endodontoid clade" of Wade et al.

Wade et al. (2001) included no Orthalicidae; their sole member of the diverse "bulimuloid" clade was a New Zealand species of *Placostylus*. Orthalicidae, exemplified by *Liguus fasciatus*, is tentatively placed on the cladogram in the position of Wade et al.'s Bulimulidae.

The correctness of the tentative placements herein of Endodontidae, Orthalicidae and Sagdidae could be tested by additional molecular studies.

Characters: Table 2 shows the distribution of character states through the taxa analyzed herein, based on the observations of Suvorov (2000). The characters and their alternative states are as follows; all are described in more detail and illustrated by Suvorov (2000: 90–99):

1. Breathing channel: (A) with pectinate folds forming a valve; (B) without valve.

2. Rectal termination: (A) open ("unclosed"), without additional structures; (B) open, with lobe; (C) open, with papilla; (D) open, with one rectal pilaster; (E) open, with two rectal pilasters; (F) partially closed; (G) fully closed.

3. Secondary ureter: (A) open ("unclosed"); (B) closed.

4. Pneumostomal excretory routes: (A) simple; (B) Y-shaped with U-shaped pilaster; (C) Y-shaped, closed; (D) Γ-shaped with anal pilaster; (E) Y-shaped with anal pilaster.

Polarity of transformation series was inferred by iterative out-group comparison of sequentially more inclusive clades and application of the "Relative Apomorphy Rule": Homologous characters found in the members of a monophyletic group and in its sister group are plesiomorphic, while homologous characters found only in the in-group are apomorphic (Brooks and McLennan, 1991, especially pp. 46–62).

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[2] The valid family-group name for the New World "Camaenidae" is Pleurodontidae von Ihering, 1912; a suprafamilial group containing Pleurodontidae and Sagdidae Pilsbry, 1895, would be correctly known as Sagdoidea.

Table 2. Distribution of character states among taxa analyzed herein. Family codes as in Table 1. See text for definition of character state symbols (A–G).

Family	Breathing channel	Rectal termination	Secondary ureter	Pneumostomal excretory route
SUC	B	G	B	A
PAR	B	E	A	D
CLA	B	E	A	D
SUB	B	D	B	A
ACH	B	C	B	E
ORT	B	F	B	D
ACA	B	C	A	E
SAG	A	C	B	C
CER	B	E	A	B
COC	B	E	A	D
ORC	B	E	A	D
CHO	B	E	A	D
PYR	B	E	A	D
ENI	B	E	A	D
BRA	B	G	B	B
HYG	B	G	A	B
HEL	B	G	A	B
END	B	A	A	A
DIS	B	B	B	B
POL	B	G	B	B
DAU	B	D	B	A
ARP	B	D	B	A
HAP	B	D	B	B
LIM	B	D	B	A
ARI	B	D	B	B

RESULTS

In Figure 2 the character states of the breathing channel are mapped on the cladogram from Figure 1. The arrangement is simple and requires only one transformation, from the absence to the presence of a valve, in Sagdidae.

In Figure 3 the character states of the rectal termination are mapped on the same cladogram. The arrangement is complex. The pattern is more intelligible if the character is first parsed into a three-state character, with rectal termination either (X) open, (Y) partially closed, or (Z) fully closed (Figure 4). Out-group comparison establishes an open termination as plesiomorphic for Stylommatophora, with three homoplastic instances of closure: once in the clade comprising Helicidae, Polygyridae, Bradybaenidae, Hygromiidae, and Sagdidae, and twice in the clade comprising Succineidae and Orthalicidae. In the latter case it is not clear that partial closure (Orthalicidae) preceded full closure (Succineidae) or vice versa; at the present level of resolution, both states appear to derive directly from the open condition.

The presence of some internal structure (one or more pilasters, a lobe, or a papilla) is plesiomorphic; an open termination without additional structures occurs only as an autapomorphic state in Endodontidae. The presence of a papilla is homoplastic, occurring in Acavidae and Achatinidae. A single rectal pilaster is homoplastic, occurring in the clade consisting of Limacoidea *sensu lato* and Arionidae and in Haplotrematidae. Presence of two rectal pilasters is homoplastic, occurring in all taxa of the orthurethran clade, in Clausiliidae, and in Cerionidae. A rectal lobe is an autapomorphy of Discidae.

In Figure 5 the character states of the secondary ureter are mapped. Out-group comparison establishes a closed ureter as plesiomorphic for Stylommatophora with four transformations to an open ureter and one reversal back to a closed ureter in the clade consisting of Limacoidea *sensu lato* and Arionidae.

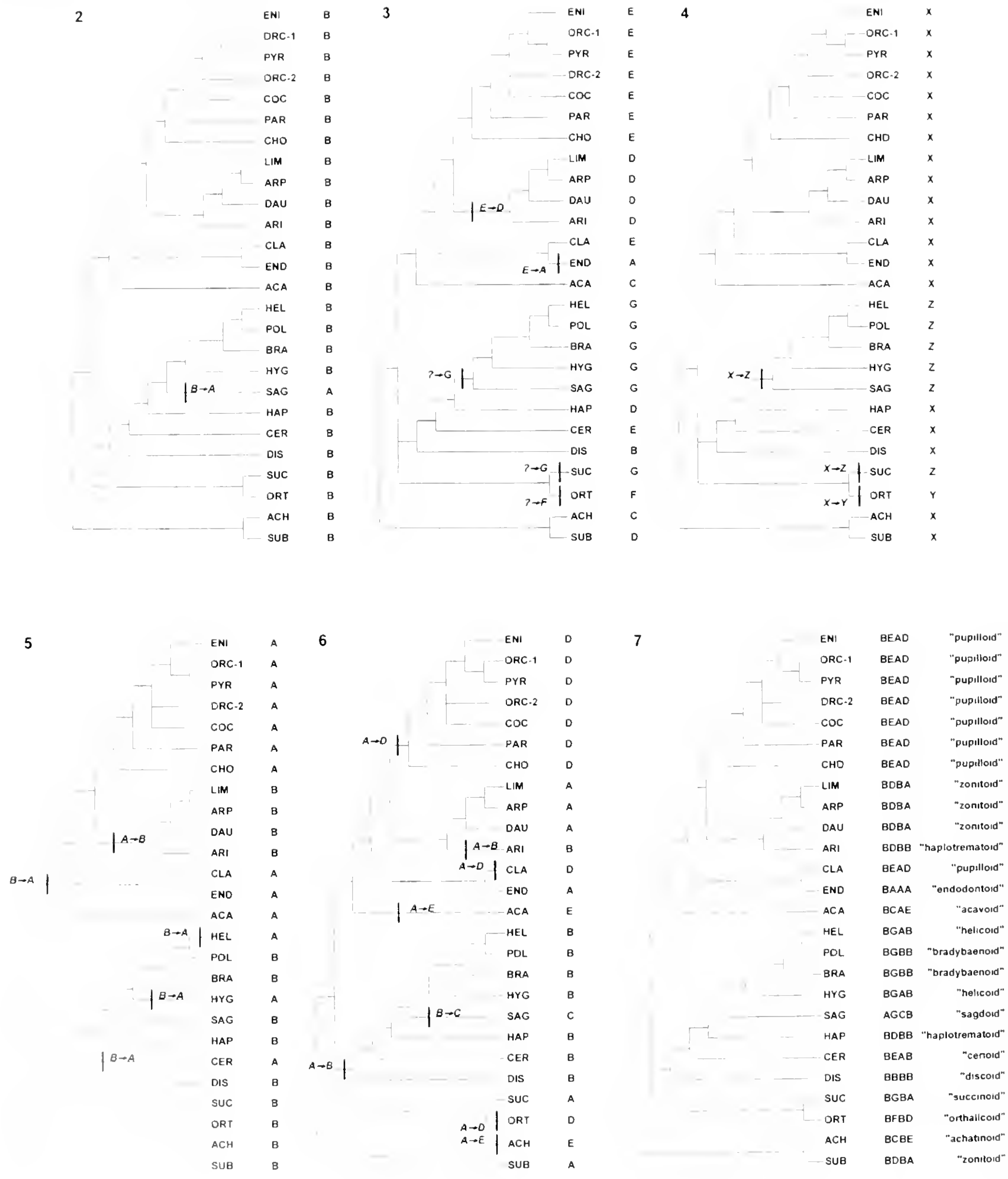
In Figure 6 the character states of the pneumostomal excretory route are mapped. Out-group comparison establishes a simple route (character state A) as the probable plesiomorphic condition, from which the four more complex states B through E arose. Character states B, D, and E show homoplasy; character state C arises autapomorphically in Sagdidae from character state B. There are no reversals from complex to simple.

DISCUSSION

It is not here assumed that a molecular phylogeny is *ipso facto* more truthful than any other, but there are several reasons why the phylogenetic hypothesis of Wade et al. (2001) is a useful standard for comparisons of the type presented here. It represents the most comprehensive molecular analysis of Stylommatophora to date, including almost 100 genera and 843 unambiguously aligned nucleotide sites. Many of its clades have strong bootstrap support. Although not necessarily determinative, many of its conclusions have intuitive appeal, such as the extent to which traditionally recognized taxonomic groups plot as monophyletic, and the geographically coherent division of others. One limitation, as pointed out by the authors themselves, is that many of the branches immediately above the "achatinoid"/"non-achatinoid" dichotomy are rather weakly supported. This could reflect either a limitation in the resolving power of the analyzed sequence or a phase of explosive cladogenesis or extinction in the history of Stylommatophora.

Inferring evolutionary history by mapping character states on this branching diagram requires no *a priori* assumptions other than that evolution has occurred. (The Relative Apomorphy Rule is not an assumption about the course of evolution but a method to enforce parsimony.) Because the underlying phylogenetic hypothesis is based on a very different data set, the possibility of circular reasoning is practically eliminated (Roth, 1996).

In contrast, the schema of evolutionary transformations of pneumostomal morphology proposed by Suvorov (2000: fig. 10) is driven by so-called functional analysis rather than by out-group comparison (Watrous and Wheeler, 1981; Brooks and McLennan, 1991). It is based strongly on *a priori* assumptions about the course of evolution ("morpho-physiological progress," "increas-



Figures 2–7. Character state distributions. **2.** Distribution of breathing channel with valve (A) and without valve (B) and location of transformation from B to A mapped on cladogram from Figure 1. **3.** Distribution of rectal termination states: (A) open ("unclosed") without additional structures; (B) open with lobe; (C) open with papilla; (D) open with one rectal pilaster; (E) open with two rectal pilasters; (F) partially closed; (G) fully closed; and location of transformations where they can be inferred from outgroup comparison. **4.** Distribution of open (X), partially closed (Y), and fully closed (Z) rectal termination and location of

ing level of differentiation — intensification of functions"), mostly articulated in the first half of the Twentieth Century (Suvorov, 2000: 99).

The analysis herein (Figure 2) indicates that a breathing channel without a valve is plesiomorphic and the presence of a valve is apomorphic. This is consistent with the transformation series inferred by Suvorov (2000: 99). The presence of a valve is autapomorphic in and diagnostic of Sagdidae. The absence of a valve is not autapomorphic for any monophyletic group.

This analysis (Figure 4) indicates that an open rectal termination is plesiomorphic and partial or full closure is apomorphic. This is consistent with the transformation from open to closed inferred by Suvorov. Suvorov referred to the condition of an open termination with various accessory structures as intermediate between the simple open and closed states (2000: 99). However this analysis (Figure 3) shows no such transformation series within Stylommatophora; the only instance of a simple open state is that of Endodontidae, which out-group comparison establishes as a transformation from a state having two rectal pilasters.

There are two homoplastic instances of closure of the rectal termination: in the clade comprising Helicidae, Polygyridae, Bradybaenidae, Hygromiidae, and Sagdidae (essentially, the clade "Helicoidea *sensu lato*" of Roth and Sadeghian, in press), and in the clade comprising Succineidae and Orthalicidae (essentially, "Clade B" of Roth and Sadeghian, in press). Closure is diagnostic of each of these clades. There are no reversals from a closed to an open state. An open rectal termination is not autapomorphic for any monophyletic group.

This analysis (Figure 5) indicates that a closed secondary ureter is plesiomorphic for Stylommatophora, with four transformations to an open ureter and one reversal back to a closed ureter in the clade consisting of Limacoidea *sensu lato* of Hausdorf (1998) plus Arionidae. This is contrary to the direction of transformation argued by Suvorov (2000: 99).

This analysis (Figure 6) indicates that a simple excretory route is plesiomorphic and that the transformation to all other, apomorphic states except C (Y-shaped, closed) occurred homoplastically. All of the complex states are derived as direct transformations from the simple state, except state C, which arises from state B (Y-shaped with U-shaped pilaster). No reversals from a complex to a simple state occur. Character state D (U-shaped with anal pilaster) is uniform throughout the Orthurethra. It also occurs in Clausiliidae and Orthalicidae but Suvorov (2000: 92) cast doubt on the homology of the condition in Clausiliidae and that in Orthurethran taxa. Suvorov's (2000, fig. 10) scenario of evolution of the pneumostomal area includes the transformations A to B (four times), A to D, B to C, and D to E. All of these transformations except D to E are found in the present analysis. The number of transformations (8) is only slightly greater than that (7) suggested by Suvorov.

Much of Suvorov's analysis is based on what he called "patterns," namely 13 observed combinations of the above character states. He named the patterns for taxa showing them (e.g., "endodontoid," "haplotrematoid"), but this practice is not very helpful when rather remotely related taxa show the same pattern (e.g., Haplotrematidae and Arionidae). His Figure 10 shows a schema of "probable" evolutionary relationships among the patterns. A plot of the patterns on the cladogram (Figure 7) gives little support for the schema and suggests instead that, for most of stylommatophoran history, the four characters of the pneumostomal area have not evolved in close concert. Rather than being basal as in Suvorov's scenario, the "endodontoid" pattern (BAAA for characters 1 through 4) is highly derived. The "pupilloid" pattern (BEAD) is uniform through Orthurethra. A similar but probably not homologous pattern occurs in Clausiliidae. The "zonitoid" pattern (BDBA) is uniform in Limacoidea *sensu lato* and, with one transformation (to BDBB) in its sister group, Arionidae; it also occurs in the phylogenetically remote Subulinidae. The clade Helicoidea *sensu lato* exclusive of Sagdidae is divided among the "helicoid" (BCAB) and "bradybaenoid" (BCBB) configurations. Other patterns are either autapomorphic or homoplastic, and it is clear that their derivation must involve separate transformations of the component characters. For this reason, I believe that the phylogeny of the pneumostomal area is better visualized in terms of individual characters (as done in the present study) than in terms of composite "patterns." For future study, the pneumostomal area characters examined by Emberton (1991) may provide additional data, if they can be coordinated with those observed by Suvorov.

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←

transformations. **5.** Distribution of open (A) and closed (B) secondary ureter and location of transformations. **6.** Distribution of excretory routes: (A) simple; (B) Y-shaped with U-shaped pilaster; (C) Y-shaped, closed; (D) U-shaped with anal pilaster; (E) Y-shaped with anal pilaster; and location of transformations. **7.** Distribution of combinations of character states for characters 1–4 ("patterns" of Suvorov, 2000).

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Cypraecassis chipolana, a new species (Gastropoda: Cassidae) from the Miocene Chipola Formation of northwestern Florida

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ABSTRACT

A new fossil gastropod of the family Cassidae, *Cypraecassis chipolana*, is described from the lower Miocene Chipola Formation of northwestern Florida. *Cypraecassis chipolana* appears to be the only known Miocene *Cypraecassis sensu stricto* from the Americas. The new species most closely resembles the Recent *Cypraecassis wilmae* Kreipl and Alf, 2000, a species endemic to tropical west America.

Additional key words: Tertiary, Neogene, fossil.

INTRODUCTION

The family Cassidae has its earliest known record in the lower Eocene. During the Miocene the family had become established throughout the warm and temperate seas of the world (Abbott, 1968). While members of the Cassidae are not uncommon in both the Recent and the fossil record, only one species of the genus most closely related to *Cypraecassis*, *Cassis delta* Parker, 1948, has previously been identified from the lower Miocene Chipola Formation of northwestern Florida. Complete or fragmentary specimens of *Cassis delta* are found in many portions of the Chipola Formation both at Tenmile Creek (the type locality) and along the Chipola River. The new species is known from a single specimen, collected on the Chipola River.

The Miocene Chipola Formation correlates in age with the Burdigalian of Europe (Vokes, 1965). Three valid species of the genus *Cypraecassis sensu stricto* have been described from the Miocene of Europe: *C. cypraeiformis* (Borson, 1820); *C. subcrumena* (d'Orbigny, 1852); *C. subtesticulus* (d'Orbigny, 1852); and one from the Miocene of East Africa, *C. pustulata* (Cox, 1927) (Abbott, 1968).

Three Recent *Cypraecassis sensu stricto*, *C. tenuis* (Wood, 1928) and *C. wilmae* from the eastern Pacific Ocean, and *C. testiculus* (Linnaeus, 1758) from the Atlantic Ocean, are known to exist in the Western Hemisphere. *Cypraecassis testiculus* also occurs in the Pleistocene of Barbados and Cuba (Weisbord, 1962) and in the Miocene of the Dominican Republic (Gabb, 1873; Pilsbry, 1922). Jung (1971) reported three incomplete specimens of an undescribed *Cypraecassis* from the Miocene Grand Bay Formation of Carriacou, West Indies. This latter taxon is morphologically similar to and may be the predecessor of *Cypraecassis testiculus senegalica* (Gmelin, 1791) from West Africa. *Cypraecassis rufa* (Linnaeus, 1758) occurs in the Indo-Pacific Region from East Africa to eastern Polynesia (Abbott, 1968).

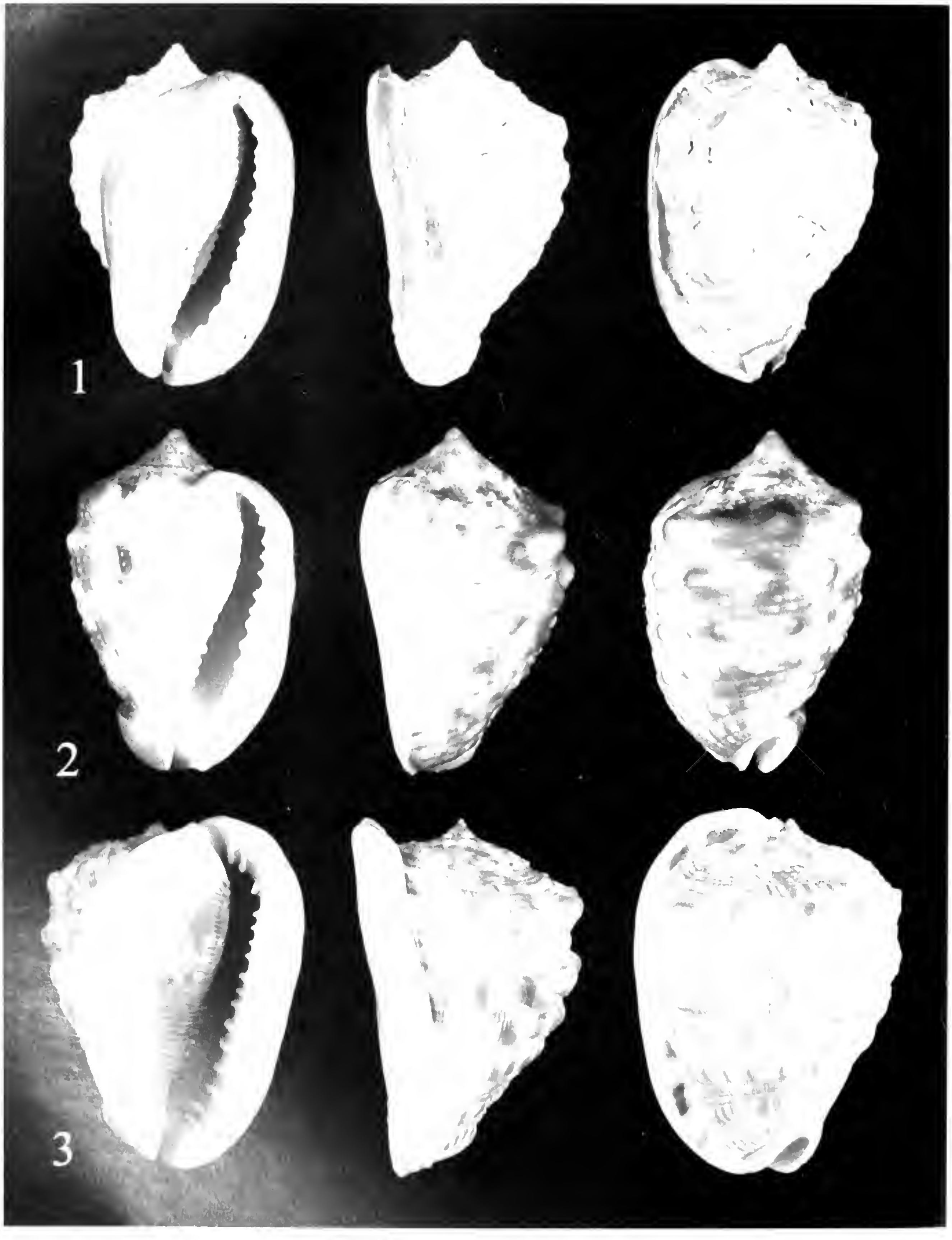
The holotype of *Cypraecassis chipolana* is deposited in the collection of the Department of Paleobiology, National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC, USA.

SYSTEMATICS

Class Gastropoda Cuvier, 1797
Superfamily Tonnacea Peile, 1926
Family Cassidae Swainson, 1832
Genus *Cypraecassis* Stutchbury, 1837
Subgenus *Cypraecassis* Stutchbury, 1837

Cypraecassis (Cypraecassis) chipolana new species
(Figure 1)

Description: Shell thick, biconical, length (holotype) 57.4 mm, width 36.2 mm. Whorls about 7 including about 3 (somewhat damaged) protoconch whorls. Spire sculpture of evenly spaced rounded pustules on inner edge of suture and a raised cord with narrow, elongate knobs. Suture slightly impressed. Dorsal sculpture consisting of 4 rows of spiral bands of 10–11, fairly rounded nodules, largest at shoulder and decreasing in size anteriorly, disappearing entirely on anterior third of dorsum. Bands of nodules interspersed with one row of greatly reduced nodules, approximately 36 on posterior row, decreasing in number and becoming 3 rows of elongate ribs covering foremost third of dorsum. Parietal shield broad, thick, elevated posteriorly at commissure with labrum; posterior canal a narrow, shallow depression. Apertural portion of parietal wall containing about 30 narrow lirations of varying lengths, crossing an axial swelling or ridge (Figure 1) on columellar wall and extending into aperture. Anterior third of parietal wall and shield slightly raised, with enlarged lirations. Anterior



Figures 1–3. Spe[illegible] lateral, and abapertural views. **1.** *Cypraecassis* [illegible] new species, holotype [illegible] Chipola River [illegible] 2. *Cypraecassis* [illegible] Kropp [illegible] width [illegible] mm, from Islas Secas, Golfo de Chiriquí, dredged [illegible] **3.** [illegible] Linnaeus, 1758, length 82.5 mm, width 57.2 mm, Indo-Pacific Region, Phyllis [illegible] Collection [illegible]

siphonal canal opening on right side of shell (in dorsal view), reflexed, deep, with chipped edge. True and false umbilicus (see Kreipl, 1997: 9) present; true umbilicus open and deep, false umbilicus closed. Outer lip thick, extending slightly into aperture and recurved upward over dorsum. Inner portion of labrum with approximately 17 single or paired stout lirations.

Type locality: Chipola River, 30°8.135′ N, 85°09.558′ W (= Tulane University locality TU 950, Chipola Formation, Chipola River, west bank about 600 m above Farley Creek (SW 1/4 Sec. 20, T1N, R9W), Calhoun County, Florida).

Type material: Holotype, USNM (Paleobiology) 517892, length 57.4 mm, width 36.2 mm.

Etymology: Named for the Chipola River, on which the type locality is situated.

Discussion: The Miocene European *Cypraecassis* may be easily separated from *C. chipolana* by the presence in the former of rib-like longitudinal plications on the dorsal surfaces of the shells or, in one species, by a smooth dorsum. The Miocene *C. pustulata* of East Africa, as the name implies, has a dorsal sculpture of much larger pustules, arranged in a different pattern than those of *C. chipolana*. *Cypraecassis chipolana* is separated from the Recent eastern Pacific *C. tenuis* by the larger, thinner shell, diaphanous parietal shield, and deeper posterior canal of *C. tenuis*. The Miocene *C. chipolana* may be easily distinguished from the Miocene to Recent *C. testiculus testiculus* of the Caribbean Region by the reticulate sculpture on the dorsum, more rounded shoulder, and thinner parietal shield of the latter. The undescribed Miocene *Cypraecassis* from Carriacou (Jung, 1971), which somewhat resembles the Recent *C. testiculus senegalica*, is differentiated from the new species by the prominent orthocline axial plicae and lack of nodules on the undescribed species. The Recent *Cypraecassis rufa* (Figure 3), ranging from East Africa to eastern Polynesia, resembles *C. chipolana*, but differs from it by the much larger shell and more rounded parietal shield of *C. rufa*. *Cypraecassis rufa* also lacks the raised portion, or swelling, on the anterior third of the parietal wall and shield of *C. chipolana*.

The species most similar to *C. chipolana* is the Recent *C. wilmae* (Figure 2), but that species has one more band of spiral knobs on the body whorl; has 8 or 9 knobs per band as opposed to 10 or 11 on *C. chipolana*; has a more rounded parietal shield; and lacks the axial swelling or ridge on the columellar wall of *C. chipolana*. On *C. wilmae*, the bands of large knobs are separated by two rows of smaller knobs or beads compared to one row on *C. chipolana*.

Features that are common to *C. chipolana* and *C. wilmae* include similar overall shapes, small adult sizes, and the unusual diagonal separation on the anterior third of the columellar callus. On the basis of morphological similarities, the possibility exists that *C. chipolana* may be the ancestor of the Recent *C. wilmae*, which became isolated in the tropical eastern Pacific with closing of the Isthmus of Panama during the middle Pliocene (Cronin et al., 1984: 43).

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My deepest appreciation to José H. Leal who critiqued the original manuscript, provided incentive, and prepared the digital images and plate. My thanks and appreciation also go to: Richard Petit for informing me that Abbott's Indo-Pacific Mollusca contained information on fossil European Cassidae; Jean Claude Six for information on fossil European *Cypraecassis*; Gary Rosenberg and Mark Kitson for reference material; Warren Blow and William G. Lyons for reviewing the manuscript; two anonymous reviewers for suggestions and pertinent information; Burke and Brooks Hayes for permission to collect on their property; Emilio Garcia for loan of specimens of *Cypraecassis wilmae*; Pamela Diegel for placing the manuscript on a computer file; and Phyllis Diegel for relevant reference material and inspiration.

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Note

Correction of a mistake introduced in the description of an aeolid nudibranch of the genus *Favorinus* Gray, 1850

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Recently, a new species of *Favorinus* Gray, 1850, from the eastern Pacific Ocean was described by ourselves in this journal (García and Troncoso, 2001). The name of this species was designated *elenalexiae* as "a juxtaposition of the names of the youngest daughters" of the authors García and Troncoso, that is, Elena and Alexia, respectively. Nevertheless, a typographic error related to the name of the species was produced in this paper. Although the species was cited as *Favorinus elenalexiae* on 22 occasions in the paper, the name also appeared twice (on pages 55 and 57) as *Favorinus elenaleixa*.

According to the International Code of Zoological Nomenclature (ICZN, 1999), articles 32.2.1 and 24.2.3 should be applied in this situation. These articles refer to the correct original spelling of a scientific name. Article 32.2.1 states: "If a name is spelled in more than one way in the work in which it was established, then, except as provided otherwise in this Article, the correct original spelling is that chosen by the First Reviser" and Article 24.2.3 states: "Selection of correct original spelling. If a name is spelled in more than one way in the original work, the first author to have cited them together and to have selected one spelling as correct is the First Reviser. The selected spelling (if not incorrect under Articles 32.4, or 32.5) is thereby fixed as the correct original spelling; any other spelling is incorrect (and therefore unavailable)." According to these Articles, acting as First Revisers we consider ***elenalexiae*** as the correct original spelling. The name represents a noun in apposition and so is indeclinable.

Since our description was published, Hans Bertsch emended the name of the species on Michael D. Miller's site on the World Wide Web. Bertsch held the view that the termination -*ae* of the name was incorrect and that it should be corrected to -*arum* (hence *elenalexiarum*) because -arum is the proper Latin suffix for a patronym established in honor of more than one female person. However, we believe that the spelling *elenalexiarum* is incorrect because the plural form should only be applied when a specific name is formed from a personal name that corresponds to two or more people who share identical names. For example, the aeolid *Flabellina marcusorum* was named by Gosliner and Kuzirian (1990) in honor of Ernst Marcus and his wife Eveline du Bois-Reymond Marcus, who first recorded this species. Accordingly, a patronym dedicated to more than one person with non-identical names, with the specific name formed by juxtaposition of the names of each person, should be considered in the singular form (i.e., *Phyllidia carlsonhoffi*, as proposed by Brunckhorst (1993), is the correct name in honor of Mr. Clay Carlson and Dr Patty-Jo Hoff). Besides this, Article 9.8 of the Code stipulates that material distributed by electronic signals (such as on the World Wide Web) is, for purposes of formal nomenclature, unpublished (ICZN, 1999). Thus, the emended name of Bertsch cannot be considered as a synonym of *elenalexiae* because it has not been included in a published work.

ACKNOWLEDGMENTS

We wish to express our gratitude to Richard C. Willan, José H. Leal, Hans Bertsch, Miguel A. Zarazaga, and José Templado for their comments during the preparation of this note.

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Book Review

Bahamian Seashells: a Thousand Species from Abaco, Bahamas.

Colin Redfern. 2001. Bahamianseashells.com, Inc., Boca Raton, ix + 280 pp., 124 plates (18 in color), 8.5 by 11 in., paperback. $114.00

The presentation of a regional molluscan fauna is constrained by its own special set of problems, including completeness, currency of nomenclature and systematics of the widest diversity of taxa, and rigor of data drawn from resources beyond the author's empiric study, such as the literature and museum records. These daunting caveats notwithstanding, Colin Redfern has nearly single-handedly chronicled a 37-year study of a marine molluscan faunule inhabiting a relatively small chain of islands, mostly on its shallow flanks, at the northern rampart of Bahamas Bank. By applying his own photographic and computer skills, Redfern has created an illustrated taxonomy that will serve workers in virtually every branch of marine malacology as well as conservation, ecology, evolution, zoogeography—not to mention serious hobbyists, who, like the author, are impelled toward a better appreciation of the natural world and its order.

The work begins with a short introduction, which indicates the geographic and ecological scope of the report, the magnitude of the material studied (108,000 well-chosen specimens, essentially all personally collected over 30 years with 16 years in residence); in the Introduction, Redfern also describes his collection techniques, which were diverse but emphasized drift and sediment material, as well as his computer and photographic techniques. He cites the nearly exclusive use of personally collected Abaco specimens in his discussions and illustrations—the only important exception being primary type material not in his possession.

There follows a 246-page systematic treatment of 1000 mollusks (777 gastropods, 10 scaphopods, 21 polyplacophorans, 211 bivalves, and 2 cephalopods). Except for the latter group, this is clearly an exhaustive treatment for such a small geographical area, and the gastropod element is stunningly diverse. Each taxon is presented with full scientific name (under the respective class, family, and subfamily), in modern-day systematic order, along with citation of illustration(s) in every instance. Exceptional are about 147 taxa, which, because of their taxonomic novelty, are identified only to the generic, rarely familial level, *comme il faut*. There follows a generally substantial paragraph that includes a detailed description, maximum size, and frequently more specific reference(s) to illustration(s) of special morphological features, and random comments on synonymy, systematics, and zoogeography at the conclusion. A shorter paragraph entitled "Occurrence in Abaco" gives a sense of frequency, bathymetric range, habitat, habits, and presence in beach drift.

A four-page glossary and an 11-page bibliography conclude the text section.

The 106 black-and-white and 18 color plates are comprised of over 2700 photographs and 75 SEMs (these latter executed by Emilio Rolán). The selection and execution are very good to excellent—rivaled only by the finest works of this sort. Particularly striking (and *de rigueur*) are the color images of all the several dozen shell-less gastropods treated in the work.

The 18-page, three-column index features reversed species names (specific epithet followed by genus name), common name, and all supraspecific taxa. Full listings of genus-species and reversed common names are not included.

The strength of this study lies in three principal areas: the underpinning of productive and well-documented field work, scholarly curation and taxonomic research, which accurately exploits virtually all modern (and some essentially overlooked classical) works, and the organization and quality of the illustrations. The synthesis of these strengths is typified in the treatment of the taxonomically nettlesome groups (e.g., Vitrinellidae, Cerithiopsidae, Triphoridae, Eulimidae, Marginellidae, Turridae, and Galeommatidae), which are depicted as thoroughly and clearly as in any modern work—and much clearer than the vast majority.

The editorial execution is as close to perfect as any work in existence. After several hours of review, only a few trivial problems were encountered. There are *Odostomia* species C and E, but no D is treated. Species 602 *Stylopsis* sp. and species 628 *Cardiopsis octona* appear to be congeneric and better assigned to *Bacteridium* Thiele, 1929. Nomenclatorial minutiae include (correction): *Eulithidium thalassicolum* (*thalassicola*), *Petaloconchus floridana* (*floridanus*), *Murexiella macgintyi* (*mcgintyi*), *Antalis ceratum* (*Cerata*), *Ctenoides scabra* (*scaber*). The bibliography is nearly exhaustive, but I was stymied by the absence of at least three references, Bavay (1922), Mörch (1876), and Nowell-Usticke (1969), which are essential because they originally describe many "forgotten" but relevant taxa that are defined for the first time in the modern literature in Redfern's work. These references were easily found in the compilation by Mikkelsen, P. M., R. Bieler and R. E. Petit (1993), a reference that was also missing.

This work is the finest regional faunal treatment to enter the annals of western Atlantic malacology in over a decade. It will prove essential to any serious student in this and related disciplines for many times that interval of time. The book is at present available only from

bahamanianseashells.com) and The Bailey-Matthews Shell Museum.

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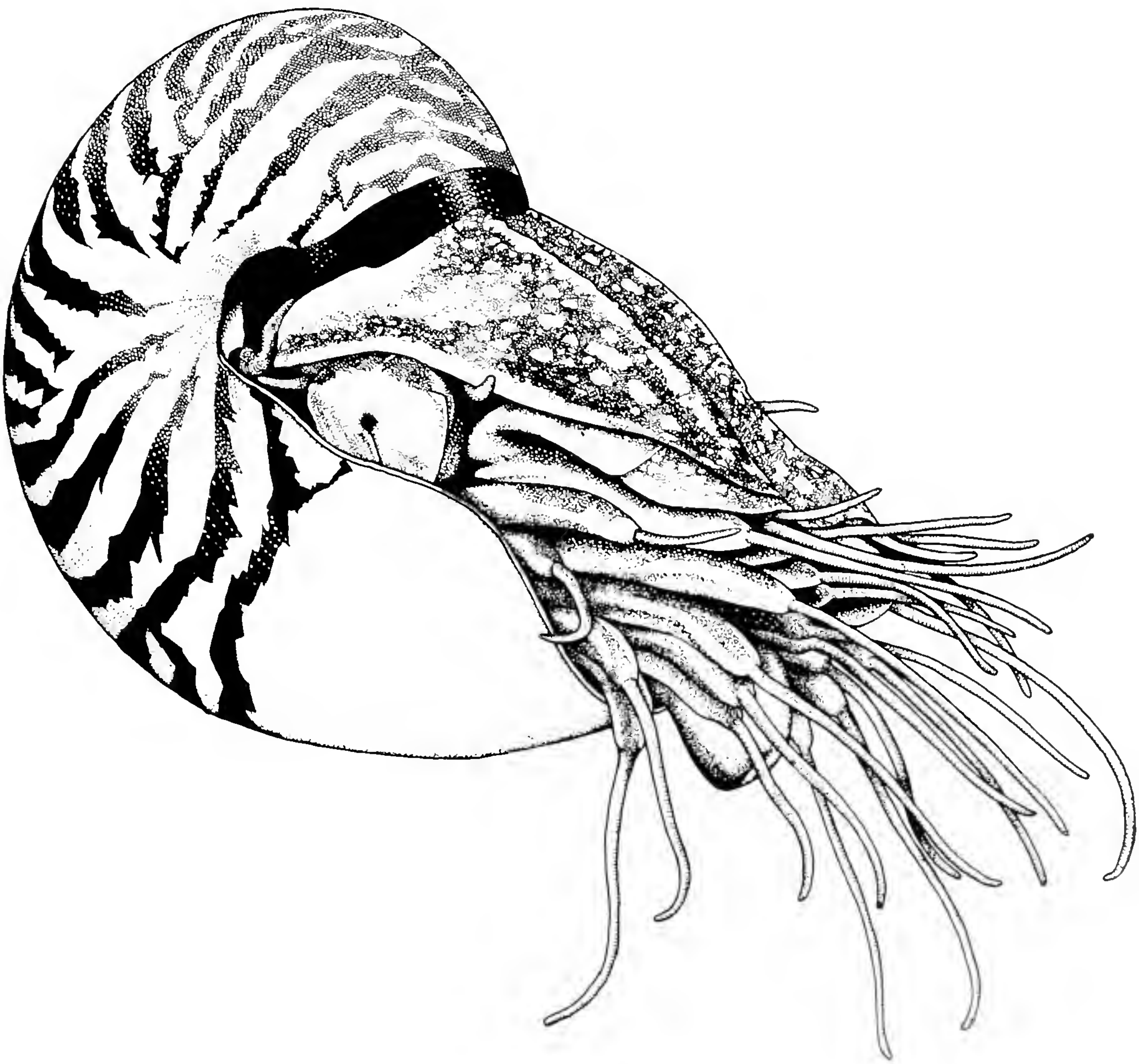

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GASTROPODA

BIVALVIA

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THE NAUTILUS publishes papers on all aspects of the biology and systematics of mollusks. Manuscripts describing original, unpublished research as well as review articles will be considered. Brief articles, not exceeding 1000 words, will be published as notes and do not require an abstract. Notices of meetings and other items of interest to malacologists will appear in a news and notices section.

Manuscripts: Each original manuscript and accompanying illustrations should be submitted in triplicate. Text must be typed on one side of 8½ × 11 inch white paper, double spaced throughout (including literature cited, tables and figure captions), with at least 1 inch of margin on all sides. All pages must be numbered consecutively. If printed on a word processor, the right margin should be ragged rather than justified. Authors should follow the recommendations of the *Scientific Style and Format—The CBE Manual for Authors, Editors, and Publishers*, which is available from the Council of Science Editors, Inc., 11250 Roger Bacon Drive, Suite 8, Reston, VA 20190, USA (http://www.cbe.org/cbe/). The first mention of a scientific name in the text should be accompanied by the taxonomic authority, including year. Latin names and words to be printed in italics must be underlined; leave other indications to the editor. Metric and Celsius units are to be used.

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